

A Remarkable Snail Fauna from Coahuila, México

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(Plates 8 to 19; 25 Text figures)

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(1) Nowhere else in North America are there 5 genera restricted to such a small area. In the Western Hemisphere the only parallel is Lake Titicaca, Bolivia-Perú, to which several genera of snails are peculiar.

(2) Nowhere else in the Western Hemisphere has the evolution of species from a common ancestor taken place in such a local area. The closest parallel among snails is found in some of the land snails of some mountains in the southwestern U.S.A., or of islands in the Pacific Ocean or West Indies, where each separate valley or limestone hill seems to have a slightly different assemblage with unique forms. Among freshwater snails such a close grouping of related species is unknown elsewhere.

(3) Most of the species are strikingly distinct in their shape or coloration. They are more like marine snails in this than like the ones to which their anatomy shows relationships.

(4) Although a number of species are restricted to a single spring, others found with them are widespread in the basin. Such an association provides a remarkable opportunity to study speciation in a natural laboratory.

(5) Spectacular though the first discoveries are, only one habitat has been reasonably well sampled – the large warm springs. Other situations, for example the subterranean rivers, have never been examined; hence still other significant findings are possible.

The traveler who visits México may well echo the popular statement "¡Como el México no hay dos!" (there are no two places like Mexico). A scientist can be more specific: ¡Como el valle de Cuatro Ciénegas no hay dos!

INTRODUCTION

THE TOWN OF Cuatro Ciénegas de Carranza lies in a valley about 40x30 km, enclosed by ranges of the Sierra Madre Oriental in central Coahuila, México. The snails of this valley are unique in North America, perhaps in the world:

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DESCRIPTION OF AREA

The valley including Cuatro Ciénegas de Carranza (Text figures 1, 2) is roughly in the shape of a horseshoe open to the south, 40 km east-west, and 30 km north-south. The horseshoe is divided by the NNW-trending spur called Sierra de San Marcos. Cuatro Ciénegas de Carranza (population 3931) is the capital of the Municipal Cuatro Ciénegas, a subdivision of the state of Coahuila. In vegetation the area is part of the Chihuahuan Desert.



Figure 1

Index map of México, showing location of Cuatro Ciénegas and states mentioned in the text.

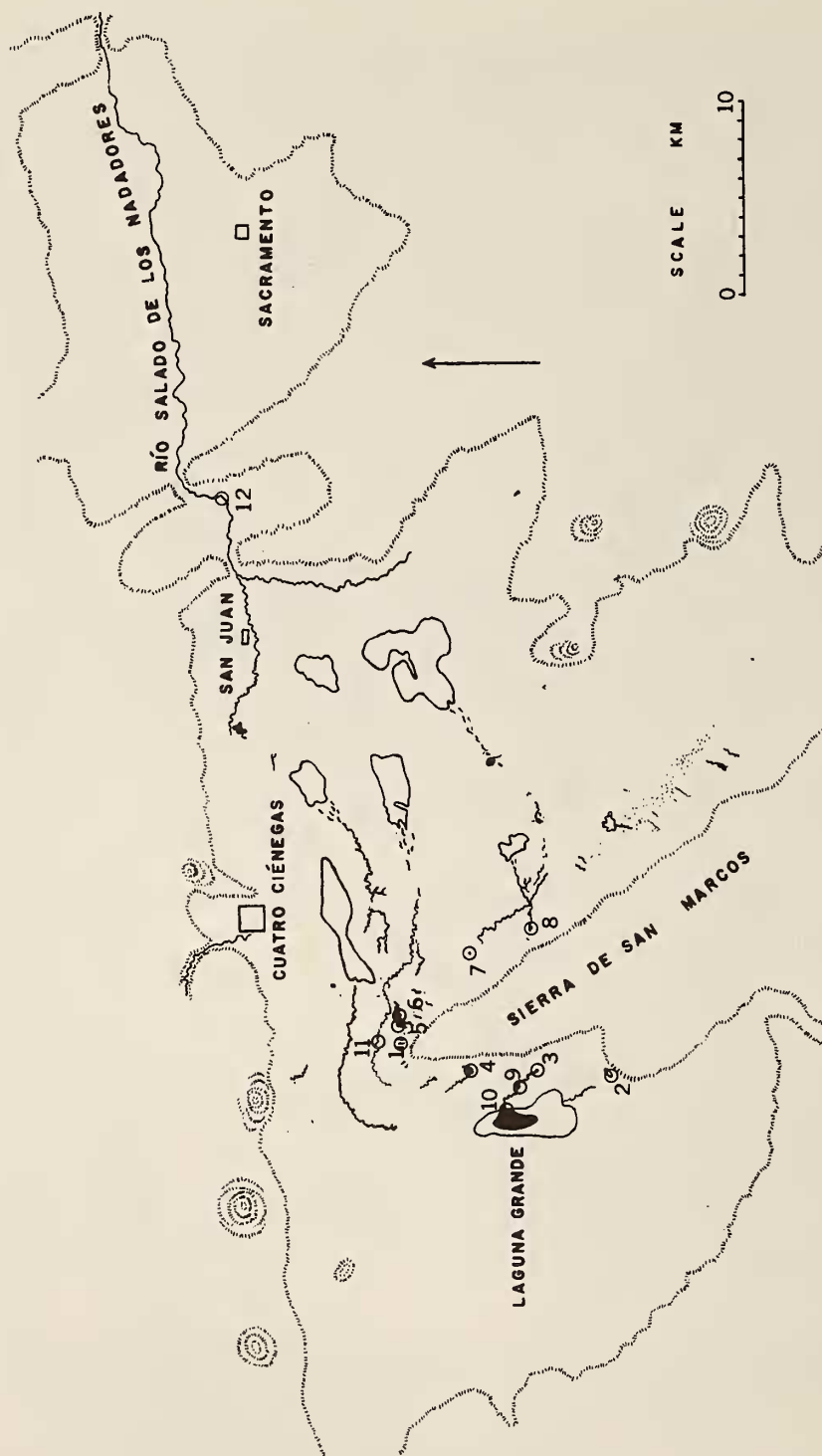


Figure 2

Index map of the valley of Cuatro Ciénegas. Mollusk localities are circled; the numbers correspond to those in the locality descriptions.
 Base prepared by W.L. Minckley, from field reconnaissance and unpublished sources.

The mountains are steep, bare limestone, all Cretaceous according to the "Carta geológica de la República Mexicana, escala 1:2 000 000, 1960." The valley lies within the Mesa del Norte (Altiplanicie Septentrional) geomorphic region of West (1964), whose paper includes an aerial photograph (fig. 9) of the basin that lacks detail useful for discussion of specific localities. Elevation of the area is a little over 700 m above sea level; the railroad station of Cuatro Ciénegas is 742 m above sea level.

The drainage of the area is both greater in volume and more complex than one expects in a desert region. Surely both of these unusual features are linked with the remarkable fauna. There are at least 5 main separate surface drainages in this small area. One includes the southern end of the western arm of the horseshoe: water flows into a saline lake, Laguna Grande (Text figure 2, locality 10), principally from the spring Churince (Text figure 2, locality 3) through the Río Churince. Waters from Pozos de la Becerra (Text figure 2, locality 4) might once have flowed into Laguna Grande, but have now been canalized northward. The second drainage is the Río Mesquites system, including localities 5-8 and 11 on Text figure 2. This was originally internal drainage but now flows through canals into the Río Grande. The third drainage is that of Río Garabatal, the farthest northwest of the tip of Sierra de San Marcos. Its originally internal basin received waters from the northern bordering mountains before canalization. The fourth drainage is that naturally tributary to the Río Grande by way of the Río Salado de los Nadadores in the northwestern corner of the Cuatro Ciénegas basin. The last drainage is the isolated lagunas of the area north and west of Rancho Santa Tecla. Isolated waters also are known besides those included in the preceding.

The previously available published maps are inadequate to show local details of the snail distribution. All mollusk localities within the valley of Cuatro Ciénegas are shown on sheet 13R-VI (Jimenez) of the Carta Geográfica de la República Mexicana (1958) 1:500 000; and on sheet NG 13 (Culiacan) of the Map of Hispanic America (American Geographical Society, 1935, scale 1:1 000 000). The locality known as El Cariño that is just outside the east edge of the valley of Cuatro Ciénegas, mollusks from which are reported herein, is included within the 14R-V (Nuevo Laredo) sheet of the Carta Geográfica de la República Mexicana.

Aside from the town of Cuatro Ciénegas de Carranza, hereafter referred to as simply Cuatro Ciénegas, few of the local place names appear on the maps mentioned, and these are mislocated. Laguna Grande is unnamed, but correctly located, on the Jimenez sheet 17 km southwest of Cuatro Ciénegas. Pozo de la Becerra is shown wrongly on that map as south of the Laguna, rather than north. El Mojarral is the local name for an area of

marshes, springs (pozos), and large spring pools (lagunas) east of the northern end of Sierra de San Marcos. On the Jimenez sheet it appears wrongly as a settlement to the west of that mountain. El Bañito of the Jimenez sheet, 12 km south of Cuatro Ciénegas, is probably the laguna known locally as Escobeda. There is no longer a settlement there. Distances and directions given herein are from a base map prepared by W. L. Minckley (Text figure 2).

Despite the negligible amount of municipal pollution, a few populations and species have already been extinguished and others are threatened. Artificial lowering of water levels by digging irrigation canals has locally destroyed some habitats and will affect others. Another, slower effect of the canal system will be the mixing of streams and populations that were naturally separate. This change has begun to affect the fishes, but in the present state of scanty knowledge of the mollusks one cannot find evidence for it, nor rule it out completely.

HISTORY OF RESEARCH

The first biologist to visit the Cuatro Ciénegas area was E. G. Marsh, Jr. who obtained a variety of vertebrates there and elsewhere in the Río Salado drainage during 1939. To him belongs the credit for discovery of the remarkable endemic fauna of fishes and reptiles. W. L. Minckley began a series of trips in 1958, resulting in visits by various herpetologists and ichthyologists, including C. L. Hubbs and R. R. Miller. HUBBS & MILLER (1965) have summarized the history of vertebrate study, and the literature to date.

The earliest collection of mollusks was made by C. L. Hubbs in 1961, and subsequently sent to me for study. From the shells it was evident that a novel fauna had been found, but no serious study could be undertaken without a chance to visit the area and collect fresh material. Continued studies by W. L. Minckley meanwhile revealed that the cichlid fish genus *Cichlasoma* included cryptic species, one of which was adapted to feed entirely on snails. Early in 1965 he brought samples of *Mexipygus*, *Mexithauma*, and *Nymphophilus* in alcohol that I identified as remarkable Hydrobiidae, and he offered an instantly accepted opportunity to visit Cuatro Ciénegas.

Thanks to the support of the University of Michigan, provided by Dr. Henry van der Schalie, I was able to join Minckley in El Paso, Texas, on April 9, 1965, for 3 days of collecting in western Texas and 4 in Coahuila.² The localities visited in the Cuatro Ciénegas area are

² Travel expenses of W. L. Minckley and students were supported by a grant for study of the genus *Cyprinodon* from the National Science Foundation, GB-2461, that thus had the unforeseen but happy result of also supporting this research on mollusks.

those considered most productive among many previously visited by Minckley. No thorough survey of the region could be made in this first visit. The notes and collections made during this trip, supplemented by the specimens collected previously by C. L. Hubbs and W. L. Minckley, were studied at the Museum of Zoology, University of Michigan. No field study of living snails with a microscope was practicable. Investigation of the anatomy of some forms, and further study of the relations between Hydrobiidae and Bithyniidae, was possible through facilities of the Hydrobiological Research Station of the University of Kyoto on Lake Biwa, Japan.³

As usual in freshwater mollusks, the investigation of the species and an attempt to put them into a framework of available knowledge revealed many uncertainties in morphology, biology and geographic distribution. Some of the snails from the valley of Cuatro Ciénegas evidently are closely related to others found outside, and I have reviewed such groups cursorily. A well-founded interpretation of the markedly distinctive genera will not be possible until the molluscan fauna of much of northern México is better known.

As study progressed, it quickly became evident that no thorough study of the fauna was possible with the material available. Two genera (*Coahuilix* and *Paludiscala*) were recognized only after return to the laboratory, and the living specimens of other genera brought back survived only a short time. Hence this paper barely puts the mollusks from the region of Cuatro Ciénegas into the available context of knowledge, diagnoses the new groups, and outlines problems for further study. The data published herein include only a part of the morphological information at hand, but are adequate to show that the new genera and subfamilies have been established as part of a search for relationships and not merely differences.

COMPOSITION OF FAUNA

As classified herein the following freshwater mollusks are known from the valley of Cuatro Ciénegas:

GASTROPODA

Prosobranchia

MESOGASTROPODA

RISSOACEA

HYDROBIIAE

Hydrobiinae?

Hydrobiidae, incertae sedis.

Cochliopinae

R⁴ *Cochliopina milleri* TAYLOR, spec. nov.

RR* *Coahuilix hubbsi* TAYLOR, gen. et spec. nov.

Littoridininae

R *Durangonella coahuilae* TAYLOR, spec. nov.

* *Durangonella*, another species?

RR *Mexipyrgeus carranzae* TAYLOR, gen. et spec. nov.

RR *M. churinceanus* TAYLOR, spec. nov.

RR *M. escobedae* TAYLOR, spec. nov.

RR *M. lugoi* TAYLOR, spec. nov.

RR *M. mojarralis* TAYLOR, spec. nov.

RR *M. multilineatus* TAYLOR, spec. nov.

* Littoridininae, incertae sedis

Nymphophilinae

RRR *Nymphophilus minckleyi* TAYLOR, gen. et spec. nov.

HYDROBIIAE?

Mexithaumatinae

RRR *Mexithauma quadripaludium* TAYLOR, gen. et spec. nov.

Paludiscalinae

RRR* *Paludiscala caramba* TAYLOR, gen. et spec. nov.

ASSIMINEAE

* *Assimineae* sp.

Euthyneura

BASOMMATOPHORA

ANCYLACEA

PLANORBIDAE

* *Drepanotrema?* sp.

PHYSACEA

PHYSIDAE

Physa virgata GOULD

The high percentage of new genera and species is evident; this aspect of the fauna is discussed under "Biogeography" below. Another striking aspect of the fauna is the dominance of Rissoacea: all but 2 of about 18 species. In part this is due to the fact that the collections are all from a limestone terrain, and mostly from springs. (Even in the mixed sedimentary-volcanic region of southwestern United States I have found that source areas of springs are usually inhabited mainly by Hydrobiidae among the snails). Yet some localities looked suitable for other mollusks; especially the clam *Pisidium* (Sphaeriidae), and snails of the genera *Bakerilymnaea*, *Fossaria* (Lymnaeidae), *Planorbella*, and *Biomphalaria* (Planorbidae) might

⁴ RRR Subfamily known only from the valley of Cuatro Ciénegas

RR Genus known only from the valley of Cuatro Ciénegas

R Species known only from the valley of Cuatro Ciénegas

* Species known only from empty shells

³ Research supported (in part) by National Science Foundation grant GB-3006.

be expected. Perhaps the composition of the water is partly responsible, as well as lack of intensive search.

BIOGEOGRAPHY

There are two general ways of studying the geographic (rather than ecologic) distribution of living organisms. One is to classify regions on the basis of the geographic range of a taxonomic group, or several groups, of animals or plants. The other is the comparative analysis of distribution, using such features as areas of greatest diversity, centers of endemism, and degrees of relationship to judge the evolution of patterns of distribution. One is descriptive, the other analytical.

Both of these methods have advantages. When dealing with a single group such as birds or reptiles, faunal provinces are useful concepts to show what large areas have generally similar faunas. Yet their boundaries are arbitrary and hence at a large scale they lose usefulness. Different organisms can evolve at different rates too, so that even combining land snails and aquatic snails to classify a region leads to difficulties. A zoogeographical scheme including both mammals and fishes could scarcely be useful on account of the different ecologic limits, modes of life, and rates of differentiation of the animals concerned, and similarly "faunal provinces" based on vertebrates are not useful for even describing, let alone understanding the distribution of mollusks. Yet since so little is known about the aquatic mollusks of northern Mexico, and tropical America in general, a regional classification into roughly defined faunal areas is useful for organizing that present knowledge.

An analysis of patterns of distribution, and the comparison of centers of endemism (TAYLOR 1966a), require more detailed knowledge than simply classifying a region, but they also yield more detailed knowledge. I have summarized the geographic distribution of the Littoridininae, the one group of snails with a fossil record pertinent to the Cuatro Ciénegas area, in order to show the value of this kind of study even when the available data are scanty.

"Faunal regions" of freshwater mollusks in northern México

Scientific knowledge of the freshwater mollusks of México and Central America up to about 1900 has been summarized in the great works by FISCHER & CROSSE (1870-1902) and MARTENS (1890-1901). Subsequent information is included in scattered papers and has never been summarized, but even today most of northern México and the adjacent U.S.A. are scarcely known. Most of the literature since 1900 is listed in Table 1. The follow-

Table 1

Literature on the freshwater mollusks of regions around the state of Coahuila. Those cited in the summaries by FISCHER & CROSSE (1870 to 1902) and MARTENS (1890 to 1901) have not been included consistently.

Drainage of Rio Grande (Río Bravo del Norte)

- a) in New Mexico, U.S.A.: F.C. BAKER (1911, 1945), BRUES (1928), COCKERELL (1896, 1902a), CRANDALL (1901:44), DALL (1896), DRAKE (1947), HENDERSON (1917, 1933), MEARNES (1907: 77), PILSBRY (1899a, 1900a, 1900b, 1906, 1916-1917), PILSBRY & COCKERELL (1900), PILSBRY & FERRISS (1906, 1909, 1917), SPRINGER (1902), WALKER (1915).
- b) in Texas and adjacent México: ALBRITTON & BRYAN (1939), F. C. BAKER (1911, 1945), CHEATUM (1935), CLENCH (1924), DALL (1896), DRAKE (1947), FERRISS (1924), HEARD (1963), LEA (1857, 1860c), LEONARD & FRYE (1962), LEONARD & HO (1960a, b), PILSBRY (1935b), PILSBRY & FERRISS (1906), SINGLEY (1893), STEARNS (1891), STRECKER (1931, 1935).

Balcones Escarpment, south-central Texas, U. S. A.

F. C. BAKER (1911, 1945), CALL & PILSBRY (1886), CHEATUM & MOUZON (1934), DRAKE (1947), GOODRICH (1942), HUBRICHT (1940), PILSBRY (1887, 1916), PILSBRY & FERRISS (1906), SINGLEY (1893), STERKI (1898), STRECKER (1935), WALKER (1909).

Chihuahua

DALL (1896), DRAKE (1953, 1956), PILSBRY (1895, 1928).

Nuevo Leon

DALL (1895: 6, 1896: 371), LEA (1860a, b, c), PILSBRY (1904), STEARNS (1891).

Tamaulipas

LEA (1857, 1860c), PILSBRY (1928), STEARNS (1893), THOMPSON (1959).

San Luis Potosí

BRANSON & MCCOY (1963), CHEATUM (1939), DALL (1905, 1908), FRIERSON (1907), HINKLEY (1907a, b), ORTMANN (1912: 271, 319, 332), PILSBRY (1909, 1910a, b, c, 1919, 1956), PILSBRY & FRIERSON (1907 - 1908), PILSBRY & HINKLEY (1907, 1910).

ing paragraphs outline the 5 geographic areas into which México could be divided according to distribution of freshwater mollusks. The endemic genera have been mentioned for each area, but no endemic species, nor all range limits of widespread genera. For comparison of the distribution of freshwater fishes, see MEEK (1904).

I. Central Plateau and Northwestern México. The only group restricted to this large area is the mussel *Arnoldina*, described from the headwaters of Río Yaqui, on the boundary between Sonora, México, and Arizona, U.S.A. The hydrobiid snail *Durangonella* is known both from this region and western México and so might be considered a second restricted genus. Some widespread northern groups, such as *Valvata* and *Anodonta* (s.s.) reach their southern limit in this region.

II. Lower Río Grande (Río Bravo del Norte) Drainage and Tamaulipas. No genera and scarcely any species are restricted to the area, outside of the Cuatro Ciénegas valley. Especially in the mussels the area marks a faunal change, for many species and genera found widely in the Mississippi Valley, and in the Gulf Coast drainage of Texas, reach their southwestern limits here. The hydrobiid snail *Cochliopina* reaches its northern limit in the lower Río Grande drainage; and the pleurocerid snail *Lithasiopsis* in Tamaulipas. So far as aquatic mollusks are known, the upper Río Grande drainage above the Big Bend resembles the closed basins to the south; it has no characteristically more southeastern or eastern species. Geological evidence (REEVES, 1965; RUHE, 1962) is consistent with this conclusion. In what is now Pecos River drainage (tributary to the Río Grande) in trans-Pecos Texas, the Hydrobiidae *Tryonia cheatumi* (PILSBRY) and "*Cochliopina*" *texana* PILSBRY mark the northeastern limit of their groups. They have no counterparts in the richer fauna of south-central Texas.

III. Río Pánuco Drainage, San Luis Potosí. Numerous species and the following genera are known only from this system:

Mussels: *Friersonia* ORTMANN, 1912 (Elliptionidae)

Snails: *Amnipila* PILSBRY, 1956 (Thiaridae)
Emmericiella PILSBRY, 1909 (Hydrobiidae)
Pterides PILSBRY, 1909 (Hydrobiidae)

Like the region of the Río Grande and Tamaulipas, this region also includes some extremes of distribution: the northern limit of *Pachychilus* (Thiaridae) and *Anodontites* (Mutelidae), the southern limit of *Lithasiopsis* (Pleuroceridae) and of the Pleuroceridae as a whole. The known fauna is richer than that of the Cuatro Ciénegas valley, and the actual fauna is probably still richer on account of the greater variety of habitats and far larger area. PILSBRY (1910c) thought the Pánuco mussels were more like those to the north than to the south.

IV. Southern México. In Vera Cruz and on southward the tropical fauna becomes evident. The family Pilidae, freshwater Neritidae, *Stenophysa* (Physidae), and other groups within the Mutelidae and Thiaridae are found.

V. Valley of Cuatro Ciénegas. If one applies uniform criteria for recognizing faunal regions, then the valley of Cuatro Ciénegas forms one by itself. None of the preceding large areas has so many restricted genera.

Endemism of mollusks in Cuatro Ciénegas valley

The contrast between the mollusks found within, and just outside, the valley of Cuatro Ciénegas is shown in Tables 2 and 3. From these it is evident that the modern topography and drainage divides have little to do with the aquatic molluscan fauna. Before the modern irrigation canals were dug, part of the Cuatro Ciénegas valley drained into the Río Salado and thence the Río Grande (Río Bravo del Norte); there was only a trivial drainage divide between this and the areas of internal drainage. The strikingly localized fauna of the Cuatro Ciénegas area then seemingly has its roots deep in the past, and is related to ancient drainage divides or other factors causing isolation and relictual survival. Perhaps this small horseshoe-shaped valley was isolated for a long time, with

Explanation of Plate 8

Pozos de la Becerra (Text figure 2, Locality 4),
 14 km southwest of Cuatro Ciénegas

Figure 1: One of the spring pools at the southwest end of Pozos de la Becerra, photographed by W. L. Minckley, 28 December, 1964, when the water level was just being lowered by a newly dug canal. Water formerly flowed to the left, where bare mud is exposed, but now drains through the canal (out of sight to right). In this view the water level had dropped 46 cm from its natural level. In December 1965 the water level had dropped a total of 113 cm.

Figure 2: Underwater view in Pozos de la Becerra, showing three different snail niches. Travertine ledges (center and right) were inhabited by *Mexithauma*, perhaps being sought by the black fish (*Cichlasoma*), right center. Soft ooze (left) was habitat of *Mexipyrhus*, and the masses of *Nymphaea* (background) the habitat of *Nymphophilus*. Photographed by W. L. Minckley, December 28, 1964. In April 1965 snails were rare, and in December 1965 none at all could be found, as a result of the drastic habitat changes.



Figure 1

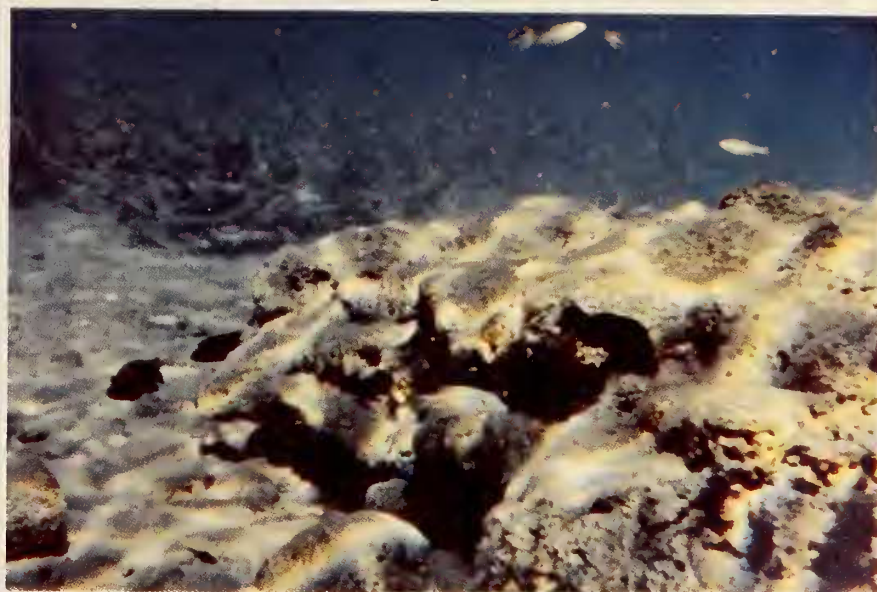


Figure 2

Table 2

Geographic relationships of snails from the valley of Cuatro Ciénegas. Species whose generic reference is uncertain are omitted.

Genus or Species	Distribution of Relatives
<i>Cochliopina milleri</i>	Nearest to <i>C. francesae</i> of Guatemala
<i>Coahuilix hubbsi</i>	Related genera in Texas and Alabama, U. S. A.; southeastern Europe to Caucasus Mountains, U. S. S. R.
<i>Durangonella coahuilae</i>	Other species of genus are in Valley of México, Colima, Durango, Michoacán
<i>Mexipyrus</i> spp.	Shares features with <i>Tryonia</i> to the west, <i>Pyrrophorus</i> to the east; genus restricted to Cuatro Ciénegas valley
<i>Mexithauma quadripaludium</i>	Genus restricted to Cuatro Ciénegas valley; no close relatives
<i>Nymphophilus minckleyi</i>	Genus restricted to Cuatro Ciénegas valley; no close relatives
<i>Paludiscala caramba</i>	Genus restricted to Cuatro Ciénegas valley; even its family uncertain
<i>Assimineae</i> spec.	Mostly found along sea-coasts
<i>Physa virgata</i> GOULD	Northern México; southwestern United States including southern Plains region

only internal drainage, before the Río Salado extended its course into the area.

The antiquity of the mollusks endemic to the Cuatro Ciénegas valley is difficult to judge since the fauna of all northern México is so poorly known. If the degree of taxonomic divergence is proportional to length of isolation, as generally assumed, then the ancestral stocks of these species and genera reach deep into the Tertiary or Mesozoic. As the fauna in the region is studied perhaps it will be possible to suggest how long the valley of Cuatro Ciénegas has been separated from the adjacent bolsons and the Central Plateau.

No direct fossil evidence is available to judge the rate of evolution of the endemic genera and species, and it

Table 3

Geographic relationships of mollusks from Río Salado de los Nadadores at El Cariño, just outside the eastern edge of the valley of Cuatro Ciénegas (Text figure 2, locality 12). Note contrast with Table 2.

Species	Distribution
<i>Pisidium compressum</i> PRIME	Most of North America, from the Pacific to the Atlantic Ocean, and Canada to central México
<i>Cochliopina riograndensis</i> (PILSBRY & FERRISS)	Lower Pecos River and Rio Grande valleys, Texas; coastal plain in Tamaulipas. The locality in Coahuila is the westernmost known occurrence
<i>Gundlachia excentrica</i> (MORELET)	Southern Texas to Guatemala, in the Atlantic drainage
<i>Helisoma anceps</i> (MENKE)	Most of central and eastern North America east of the Rocky Mountains. The locality in Coahuila is the southernmost known occurrence
<i>Physa virgata</i> GOULD	Northern México; southwestern United States including southern Plains region

is unlikely that a significant fossil record of freshwater mollusks will be found in the Cuatro Ciénegas valley. The reclassification of the subfamily Littoridininae of the Hydrobiidae (see below) nevertheless provides suggestive evidence of the rate of generic divergence. Most of the genera are entirely or almost allopatric (Text figure 14), from which it seems that their taxonomic differentiation is significantly linked with geographic isolation. *Mexipyrus*, restricted to the Cuatro Ciénegas valley, shares characters of both *Tryonia* (late Oligocene or early Miocene to Recent) and *Pyrrophorus* (early Pliocene to Recent). If one assumes that these 3 genera have diverged from a common ancestor for the same length of time, then the origin of *Mexipyrus* goes back to early Tertiary times. Whether *Mexipyrus* has always been restricted to the valley of Cuatro Ciénegas, or only retains part of a formerly greater distribution, is uncertain since the region is so poorly known. The possibility that there has been a freshwater habitat in the area continuously suitable for snails since middle or early Tertiary time should nevertheless be considered seriously.

The time required for the differentiation of the local forms of *Mexipyrigus*, restricted to single springs or streams, can only be estimated by comparison with the rates of other hydrobiid snails. As it happens, virtually none of the living species of Littoridininae has a useful fossil record, and hence these estimates are not based on species related closely to *Mexipyrigus*.

Among Hydrobiidae in the western U.S.A., *Lithoglyphus* species (Lithoglyphinae) generally have the longest range. *L. hindsii* (BAIRD) is known from a late middle Pliocene or early late Pliocene assemblage in Oregon (TAYLOR, 1966a). *Lithoglyphus columbianus* (PILSBRY) is known from the middle Pliocene, and *L. virens* (LEA) from the middle or perhaps early Pliocene (U.S. Geological Survey collections; unpublished). In correlation with this longer range the species have geographic distributions that are wider and transcurrent to the ranges of other Hydrobiidae. The one living species of Littoridininae that has been found in Tertiary rocks is *Tryonia imitator* (PILSBRY), recorded by OAKESHOTT (1958:67-68) from the upper Miocene and lower Pliocene Mint Canyon Formation in Southern California.

Other western American Hydrobiidae mostly have no fossil record, or cannot be specifically identified from their shells. The distribution of the living species is generally accordant with biogeographic patterns that seem no younger than late Pliocene in age (TAYLOR, 1966a). Judging by this analogy the localized species of *Mexipyrigus* have differentiated since about the late Pliocene or earliest Pleistocene, i.e., during about 2-3 million years.

One of the more interesting biological studies possible in the valley of Cuatro Ciénegas is the comparison of rates of evolution of different animals living in substantially the same habitat: the fishes, turtles, snails, Crustacea, and so on. The mere naming and describing, let alone study, of these groups has scarcely gotten underway. The snails may prove to have the most nearly complete fossil record of these animals in the area, and hence they will be of special value in estimating rates of differentiation.

Despite the early stage of scientific study of the Cuatro Ciénegas area, there is good evidence that the habitats of the snails have been there for a long time. The speciation in *Mexipyrigus* even suggests that individual large springs or groups of springs might have antiquity of a few million years. Such a length of isolation is under-

standable in an arid climate, like that of the present, but annual rainfall was almost surely substantially greater during the Pleistocene. The only area in North America where a considerable fossil record for much of this interval is available is in the southern Great Plains of the U.S.A.; there the present, living fauna is sparser than all of the fossil assemblages, and the modern semiarid climate seems to be a geologically late phenomenon (TAYLOR, 1965). If climatic change was correlative in Coahuila, then the modern arid climate might have developed only in the last 10 000-20 000 years. Nevertheless in a limestone terrain the porous soil does not retain moisture long, and even in a more humid climate the Cuatro Ciénegas valley probably had much its present surface aspect, though with increased flow of springs and streams, and increased underground flow out of the valley. This supposition is consistent with the fact that most of the unique, endemic organisms in the valley are strictly aquatic, or are marsh dwellers; and it is consistent with the evidence of the snails that their habitats have been persistent for millions of years. Surely not all the endemic species in the valley—not even the snails—have changed at the same rate, but the interpretation of evolution in fishes, reptiles, and other groups should not rest merely on the assumption of a certain rate of differentiation, nor on inferred effects of climatic change during the Pleistocene.

LOCALITIES AND HABITATS

Descriptions of the localities and habitats, and lists of associated species, are given below. Numbers correspond to those on the locality map (Text figure 2). Four general types of habitats of freshwater mollusks have been sampled: small spring, large spring, laguna, and stream. Physico-chemical data for most of the mollusk localities cited herein are available in MINCKLEY & COLE (1966).

SMALL SPRING (POZO)

1. Only one natural locality of this type has been sampled, a spring tributary to the area of marshes and lagunas known locally as El Mojarral, 1.7 km due east of the tip of Sierra de San Marcos, 11 km southwest of Cuatro Ciénegas; W. L. Minckley, 13-IV-1965. A bottom sam-

Explanation of Plate 9

West Laguna in El Mojarral (Text figure 2, locality 5) 1.7 km east-northeast of the northern tip of Sierra de San Marcos. *Mexipyrigus mojarralis* TAYLOR, spec. nov., is found only here. Underwater photographs by W.L. Minckley, April 1965. *Mexipyrigus* lives in the soft ooze, *Nymphophilus* on the *Nymphaea* leaves. The larger fishes in both photographs are the cichlid, *Cichlasoma*.



Figure 3



Figure 4

ple of black organic ooze and abundant shells, all dead, yielded two species.

* *Durangonella* spec.

* R⁵ *Paludiscala caramba* TAYLOR, gen. et spec. nov.

2. Rancho San Marcos, 20 km south-southwest of Cuatro Ciénegas. A spring here has been substantially modified for irrigation, and was not sampled. In the brief visit a collection was made from the shallow (less than 5 cm) water in the livestock-trodden muddy area around the spring. The only vegetation in these shallows was *Chara* and sedges. Snails were noticeably restricted to the marginal shallows. D. W. Taylor, 14-IV-1965.

Physa virgata GOULD

LARGE SPRING (LAGUNA)

A number of large warm springs in the valley of Cuatro Ciénegas issue through travertine-lined natural "pipes" and form pools 50-100 m in diameter, locally known as "lagunas" (Plate 8, Figure 1). The habitats in each of these are generally similar, and so are the mollusks in the 6 springs that have been examined.

Characteristically the deepest area is 5-10 m below the water surface, and most of the bottom is covered with 3-6 cm of flocculent ooze, composed mainly of snail feces, lying on a firmer substrate of shells, shell fragments, and clay. The water is clear, and only at a distance of 10-15 m does an object appear a little hazy. One who first dives in one of these large, clear lagunas with the numerous cichlid fishes (*Cichlasoma* spp.) (Plate 9, Figure 3) that are boldly colored and change color with startling speed, is immediately struck with the impression he is in an aquarium. The constant flow of water, lack of turbidity, and the virtual absence of plankton make these spring-pools conspicuously more clear than the ponds and lakes that are more nearly closed systems.

The fishes include representatives of 7 families, and at least 15 species occur in the laguna habitats of the basin. These fishes are ecologically diverse, occupying most recognized trophic levels throughout the habitat. One may surmise that this diversity in the fishes is somehow correlated with the ecological differentiation of the snails.

Beyond a depth of 1-2 m the only conspicuous higher plant is a water-lily, *Nymphaea*. These commonly grow in patches (Plate 8, Figure 1; Plate 9, Figure 3) to a depth of several meters but beyond about 0.5 m do not send their leaves to the surface to form lily-pads. Instead the leaves remain in the juvenile, half-unrolled state at depth, and the scattered patches of lilies grow to a height of only

about 30 cm. This growth-habit of the *Nymphaea* is one of the bizarre biological aspects of the lagunas.

At a depth of less than 1-2 m the individual lagunas differ more than beyond that limit. The size and shape of each pool, and the abundance of sedges and marginal aquatic plants vary; perhaps also the pools are in different stages of ecological succession. The seasonal fluctuations in flow of the springs change the water level through a few cm, and wave action washes fine material into deeper water, so that a hard substratum (mostly tufa, sometimes rock) is exposed locally. In areas of stronger current the bottom is mainly composed of white shells and shell fragments mixed with rounded pieces of tufa, of the texture of coarse sand and fine gravel.

Three genera of snails are consistently found in all the springs, always in the same habitat. *Mexipyrus* is common to abundant in the upper 1-2 cm of the flocculent ooze bottom, in all depths of water. Presumably it digests the microorganisms (mainly bacteria?) in this material; there seems to be no other food source. The bottom is so loose in texture that at least locally these snails probably move about little if at all. They were always in the bottom, not visible at the surface.

Nymphophilus lives on the *Nymphaea* leaves, rarely on the lower surfaces of blocks of tufa. The rare specimens collected from the loose-textured bottom with a sieve were adjacent to *Nymphaea*, seemingly having fallen off. No *Nymphophilus* were seen on exposed surfaces: neither on the upper surfaces of submergent leaves, nor on the stems or lower surfaces of floating leaves. All collecting was done by day, hence this distribution may not be characteristic of the night. In any case it might be a consequence of fish predation on easily visible snails, rather than of food preference by the snails. Field and laboratory observations indicate *Nymphophilus* may eat the *Nymphaea* leaves themselves as well as epiphyton.

Mexithauma is ordinarily found on a hard substratum (stones or tufa), sometimes on a firm shelly mud bottom. Diatoms are common on the surface of its shell, whereas *Mexipyrus* shells are always completely clean, and those of *Nymphophilus* are mostly clean with some algae. Seemingly *Mexithauma* browses on algae, or eats the organic material or microorganisms in the surficial layers of mixed detritus in shallow water.

Collecting in these large springs was done manually (by picking snails off blocks of tufa, or *Nymphaea* leaves), and with sieves; both by wading in the shallower areas and diving to depths of generally 3-4 m. A fine-mesh screen (ca. 1 mm) was used briefly at most localities, but tiny snails such as *Coahuilix* were overlooked, or not found in this sampling. Hence a coarser meshed screen (ca. 2 mm) was used for nearly all bottom-sampling.

⁵ R Species restricted to this locality

TL Type locality of species found also at other places

* Species represented by empty shells only

The most convenient way to collect proved to be holding the screen so as to skim off the upper 1-2 cm layer of bottom while swimming. In this way large series of *Mexipyrus* were collected, but in retrospect (having discovered the *Coahuilix* specimens since the field work) rare, tiny shells would have been missed. Furthermore, I found it difficult to work for long at depths of over 6 m, and thus could not give the limey surfaces in and around the spring vents a careful search. Such places are the most likely situation in which to find traces of a special subterranean fauna, but SCUBA (self-contained underwater breathing apparatus) equipment at least will be necessary for collecting there, and still more elaborate apparatus for the subterranean conduits where no light penetrates.

In the biota of the lagunas these 3 genera of snails—*Mexipyrus*, *Mexithauma*, and *Nymphophilus*—seemingly make up the greater part of metazoan standing crop, although quantitative sampling has not yet begun. Other animal groups—for example insect larvae or adults, Crustacea, annelids, and planarians—are absent or far less conspicuous than in ponds of similar size in which I have collected in the U.S.A. Fishes are conspicuous on account of their size, and are locally numerous. So far as I can judge from a brief visit, the food chains in these lagunas are remarkably short and simple: algae and benthic microorganisms → snails → fishes. One of the cichlids is the only fish that eats snails regularly, and it is present in all the major lagunas. From the relative abundance of broken shell fragments to empty, unbroken shells in sieve samples I would guess that locally over 75% of the snails that reach maturity are eaten by fishes.

3. Laguna Churince, 16 km southwest of Cuatro Ciénegas. Water temperature ranged from 25.9-28.9°C on 6 occasions, measured by W. L. Minckley. Most collecting was done in the outflow of the spring, that is in the upper end of Río Churince (Plate 11, Figure 9). The laguna is about 50 m in diameter and contains *Nymphaea* and *Nymphophilus*, both lacking in the outflow. Río Churince here is a clear, slow stream about 2 x 0.5 m, with a soft mud bottom and the usual border of sedges. D. W. Taylor, 12-IV-1965.

R^a *Mexipyrus churinceanus* TAYLOR, gen. et spec. nov.

^a For explanation of symbols see footnote ^a above

Mexithauma quadripaludium TAYLOR, gen. et spec. nov.

Nymphophilus minckleyi TAYLOR, gen. et spec. nov.

* cf *Succinea*

4. Pozos de la Becerra, 14 km southwest of Cuatro Ciénegas (Plate 8, Figures 1, 2). "Prior to December 1964, Pozos de la Becerra was one of the largest and most complex aquatic habitats in the Cuatro Ciénegas basin. The laguna was elongate and irregular in shape, with depths ranging to more than 10 m at the largest spring inflows. In areas of inflow the bottoms were of gravel and rubble. Other areas had bottoms of deep calcareous silt; most silt bottoms were covered by dense beds of waterlily (*Nymphaea*). The laguna originally measured about 25 m in width at its narrowest place, ranging to more than 150 m wide, and was perhaps two km long. Water was always extremely clear. Temperatures taken in the sources on seven different occasions ranged from 29.4 to 32.2°C. Water levels did not change perceptibly in the period 1960-64, and one estimate of discharge was about 1.34 m³/second at the outlet channel.

The laguna suffered some modification in 1961 through construction of a bathing facility. In 1964, however, the laguna was drastically modified by construction of a canal, and the water level fell 46 cm in about two days. In April 1965, the downcutting of the uncontrolled canal outlet had apparently stabilized, with the laguna surface lowered more than a meter. This resulted in drainage of extensive marshes that were associated with the spring, and reduced the over-all surface of water and marsh from perhaps 10 km² to less than 0.2 km². Swimmers had muddied the laguna in April 1965, and the silty bottoms had been greatly disturbed. Many formerly gravel bottoms were silted and most of the *Nymphaea* beds were dried or uprooted. Only the inflows of the largest springs remained clear of silt" (COLE & MINCKLEY, 1966:20).

One of the drastic effects of the drop in water level was the concentration in a small volume of water of the fishes, with several-fold increase in competition for food. In April, 1965, the snails that W. L. Minckley had previously found common (*Mexipyrus*, *Mexithauma*, *Nymphophilus*) were all rare, and scarcely any of them were found alive in spite of persistent search. The snail-eating cichlids, *Cichlasoma*, were seemingly starving; they had sunk-

Explanation of Plate 10

West Laguna in El Mojarral (Text figure 2, Locality 5), 1.7 km east-northeast of the northern tip of Sierra de San Marcos.

Mexipyrus mojarralis TAYLOR, spec. nov., is found only here.

Figure 5: Edge of laguna, showing juvenile *Nymphaea* and small tufa knobs in water 5-20 cm deep. *Mexithauma* was found on the lower surfaces of these tufa blocks.

Figure 6: View eastward showing most of the length of the laguna.

In the right distance is visible the western end of East Laguna to the south (type locality of *Mexipyrus multilineatus* TAYLOR, spec. nov.). Water issues from large vents out of the picture to the left; most of the water flows out through a large vent at the far end of the laguna, but there is a minor surface outflow not visible in this view. A patch of *Nymphaea* growing in about 2 m depth is at left center; a ledge of tufa in the center foreground.



Figure 5



Figure 6

en bellies. In December, 1965, thorough search by Minckley revealed no live snails.

Collections by W. L. Minckley, 28-XII-1964; D. W. Taylor, 14-IV-1965.

Mexipyrus churinceanus TAYLOR, gen. et spec. nov.

Mexithauma quadripaludium TAYLOR, gen. et spec. nov.

Nymphophilus minckleyi TAYLOR, gen. et spec. nov.

A sample from the surface of the marly bottom in the (former, now drained) northernmost pool was collected by C. L. Hubbs, 6-IV-1961. It yielded the preceding 3 species as well as the following:

R* *Assimineia*

R* *Coahuilix hubbsi* TAYLOR, gen. et spec. nov.

R* Littoridininae, incertae sedis

R* *Drepanotrema*?

5. West Laguna in El Mojarral, 1.7 km east-northeast of the northern tip of the Sierra de San Marcos (Plates 9, 10). The springs emerge through vents up to 1 m in diameter at the north-western end of a laguna about 25 x 100 m, up to 7 m deep. Nearly all of the water flows out through a large vent at the southeastern end of the laguna; thus there is only a trivial surface-water outflow, that runs into the next laguna (locality 6). Water temperature was 32.8°C on 2 occasions, measured by W. L. Minckley. *Nymphophilus* was sparse and small in the patches of *Nymphaea* (Plate 9) that here was less abundant than in other lagunas. *Mexithauma* was rare on the lower surfaces of tufa at the edge (Plate 10, Figure 5). *Mexipyrus* was abundant in the upper 1-2 cm of the soft, flocculent ooze bottom. D. W. Taylor, 13-IV-1965.

R *Mexipyrus mojarralis* TAYLOR, gen. et spec. nov.

Mexithauma quadripaludium TAYLOR, gen. et spec. nov.

Nymphophilus minckleyi TAYLOR, gen. et spec. nov.

6. East Laguna in El Mojarral, 1.9 km east-northeast of the northern tip of Sierra de San Marcos. The western end of this laguna receives a small surface flow from the preceding (locality 5), and can be barely seen in the right distance of Plate 10, Figure 6. The same habitats were represented here as at the preceding, nearby locality; but this laguna differs by being about 300 m long, and shallower, with much of its area 1-2 m deep, supporting scattered emergent sedges as well as *Nymphaea*. It is remarkable that the 2 nearby lagunas, only 300 m apart, with similar habitats, have obviously different forms of *Mexipyrus*. D. W. Taylor, 13-IV-1965.

R *Mexipyrus multilineatus* TAYLOR, gen. et spec. nov.

Mexithauma quadripaludium TAYLOR, gen. et spec. nov.

Nymphophilus minckleyi TAYLOR, gen. et spec. nov.

7. Laguna Escobeda, 12 km south of Cuatro Ciénegas. The spring is now only a conical pool about 20 m in diam-

eter, 10 m deep, whose natural level was evidently 2 m higher before the present outlet was dug. Water temperature was 34.4°C on the 9 occasions when measured by W. L. Minckley. *Mexipyrus* was abundant in the soft flocculent ooze of the bottom, and was the only snail found alive. White, empty shells of *Mexithauma* and *Nymphophilus* are common in the spring flow, but *Mexipyrus* is the only snail living there. Aquatic vegetation is almost nil; no *Nymphaea* remains; fish are scarce. Clearly the biological diversity and productivity of the laguna have been drastically reduced, by the elimination of large areas of shallow, vegetated water. W. L. Minckley, 31-XII-1964; D. W. Taylor, 15-IV-1965.

R *Mexipyrus escobedae* TAYLOR, gen. et spec. nov.

* *Mexithauma quadripaludium* TAYLOR, gen. et spec. nov.

* *Nymphophilus minckleyi* TAYLOR, gen. et spec. nov.

8. Laguna Tío Cándido, 14 km south of Cuatro Ciénegas. The laguna is 250-300 m long, and up to 4 m deep. Water temperature at the surface ranged from 21.1 to 27.8°C on four occasions when measured by W. L. Minckley. Irrigation development has lowered the water level slightly, but seemingly there have been no drastic changes in the snail fauna since the 3 characteristic genera are present. The bottom is more thickly vegetated with *Nymphaea* than other lagunas, and both *Nymphaea* and sedges can be seen at the surface around the edges (Plate 12, Figure 9). *Mexipyrus* was in the soft mud bottom, as elsewhere. *Nymphophilus* was regularly on the under side of *Nymphaea* leaves, and also on the lower surfaces of tufa and stones with an epiphyton. *Mexithauma* was mostly on stones or a firm substratum covered with a thin (about 1 cm) layer of mud, so that the snails were invisible; but rarely they were on *Nymphaea* too. D. W. Taylor, 15-IV-1965.

This is the type locality of the turtle *Trionyx ater* WEBB & LEGLER (1960).

R *Mexipyrus carranzae* TAYLOR, gen. et spec. nov.

TL *Mexithauma quadripaludium* TAYLOR, gen. et spec. nov.

Nymphophilus minckleyi TAYLOR, gen. et spec. nov.

LAGUNA

Two localities are in what an English-speaking American would call ponds or lakes, but locally they are called lagunas like the preceding group of large spring sources.

9. Unnamed laguna about 1.0 km northwest of Laguna Churince, 16 km south-southwest of Cuatro Ciénegas. The laguna is about 250 m long, 65 m wide, with a soft calcareous ooze bottom and pebble to cobble-sized discoidal to irregular blocks of tufa at the actively eroding edge.

Cattails (*Typha*) grew in protected places, sedges around the edge. *Nymphophilus* was sparse on the lower surfaces of tufa blocks, and another hydrobiid rare. The habitat was similar to that at the edge of West Laguna in El Mojarral (Plate 10, Figure 5), but no *Nymphaea* was found. D. W. Taylor, 14-IV-1965. The banks had been eroded about 12-18 m locally by December, 1965, according to observations by W. L. Minckley.

Nymphophilus minckleyi TAYLOR, gen. et spec. nov.

Hydrobiidae, incertae sedis

10. Laguna Grande, at mouth of Río Churince, about 17 km southwest of Cuatro Ciénegas. This laguna is the sump of Río Churince and has no surface outlet. It is about 2 km long, 1 km wide, with a high magnesium chloride content and dunes of nearly pure gypsum on the west. At the mouth of the river, in the middle of the east side of the laguna, the *Scirpus* bordering the stream extended a little way into the laguna but elsewhere the only vegetation was isolated individuals of a tiny *Chara*, only about 3 cm high. Along the edges of the laguna at a depth of less than 20 cm clumps of grasses formed islands 2-3 m in diameter. The bottom was soft mud in the upper 5-10 mm of which *Durangonella* was common. The specimens collected came from a depth of about 5-30 cm, but the snails might occur throughout the laguna. No *Durangonella* were found within about 4-5 m of the mouth of Río Churince, either because of lowered salinity or a combination of factors. D. W. Taylor, 14-IV-1965.

The species described from this laguna is probably re-

stricted to it, but the anatomy of *Durangonella* from elsewhere in the valley is unknown.

R *Durangonella coahuilae* TAYLOR, spec. nov.

STREAM

11. Río Mesquites 9 km southwest of Cuatro Ciénegas, at the road running from Cuatro Ciénegas around the northern end of Sierra de San Marcos (Plate 11, Fig. 8). The habitat is much like that in the outflow of Laguna Churince; see explanation of Plate 11 for comparison of these 2 localities. The stream is generally about 2 m wide, 1-1.5 m deep, flowing between steep banks with a clear, steady current. *Cochliopina* was mostly in the soft mud of backwaters where it was associated with *Mexipyrus*; the latter was also in the main stream where *Cochliopina* was absent. *Nymphophilus* was common on the lower surfaces of the submerged clusters of *Nymphaea* leaves, as in the lagunas. The bottom of soft mud and gravel with scattered stones and dead wood gave the habitat the appearance of being much like those found widely in the U.S.A., but lacked mollusks that one would expect. There were no Sphaeriidae, Lymnaeidae, or Planorbidae found in spite of search for them. The species represented by empty shells only are known by single specimens in each case. D. W. Taylor, 13-IV-1965.

R *Cochliopina milleri* TAYLOR, spec. nov.

* *Durangonella*

* Hydrobiidae, incertae sedis

R *Mexipyrus lugoi* TAYLOR, spec. nov.

Explanation of Plate 11

Río Churince and Río Mesquites

The localities are about 12 km apart, and look similar on the ground as well as in these illustrations. Yet they have no species in common. Figure 7: Río Churince at its source about 20 m downstream from Laguna Churince (Text figure 2, Locality 3), 16 km southwest of Cuatro Ciénegas. View northwestward toward Laguna Grande (not visible). About 0.5 km in the distance is an intermediate laguna (Text figure 2, Locality 9) also not visible in this view, where *Nymphophilus* was collected. In the short segment of Río Churince shown here *Mexipyrus churinceanus* TAYLOR, spec. nov., was abundant in the muddy bottom; *Mexithauma* was common on the firmer parts of the bottom and on the steep walls of the stream. *Nymphophilus* was found living in the laguna upstream, but not

here. Water depth about 0.5 m.

Figure 8: Río Mesquites (Text figure 2, Locality 11), 9 km southwest of Cuatro Ciénegas. The road crosses the stream at the right (just out of the picture) and runs south-southwest around the northern end of Sierra de San Marcos (center skyline). Río Mesquites has greater flow than Río Churince, with more rapid current, and is deeper (0.5 - 1.0 m). *Nymphaea* grows here in submerged masses as in the lagunas. The fauna differs from that found above (Figure 7) by having *Cochliopina*, *Nymphophilus*, and a different *Mexipyrus* (*M. lugoi* TAYLOR, spec. nov.); and by lacking *Mexithauma*.

Explanation of Plate 12

View southeastward across Laguna Tío Candido (Text figure 2, Locality 8), 14 km south of Cuatro Ciénegas.

Eastern slope of Sierra de San Marcos at right. Water depth 3 - 4 m. Floating pads of *Nymphaea* and emergent sedges are visible toward the edges in shallower water. Type locality of *Mexithauma quadri-paludium* TAYLOR, gen. et spec. nov.; and *Mexipyrus carranzae* TAYLOR, gen. et spec. nov.

Figure 10: Río Salado de los Nadadores at El Cariño de la Montaña (Text figure 2, Locality 12), 20 km east of Cuatro Ciéne-

gas. The locality is just outside the northeastern edge of the valley of Cuatro Ciénegas, in a stream naturally tributary to the Río Grande (Río Bravo del Norte). The fauna is entirely like that of the Río Grande drainage; none of the new local species of the Cuatro Ciénegas area was found here. *Helisoma anceps* was found only in the small spring pool in the center foreground; the other species were both in the spring and in sheltered situations along the edge of the stream.



Figure 7



Figure 8



Figure 9

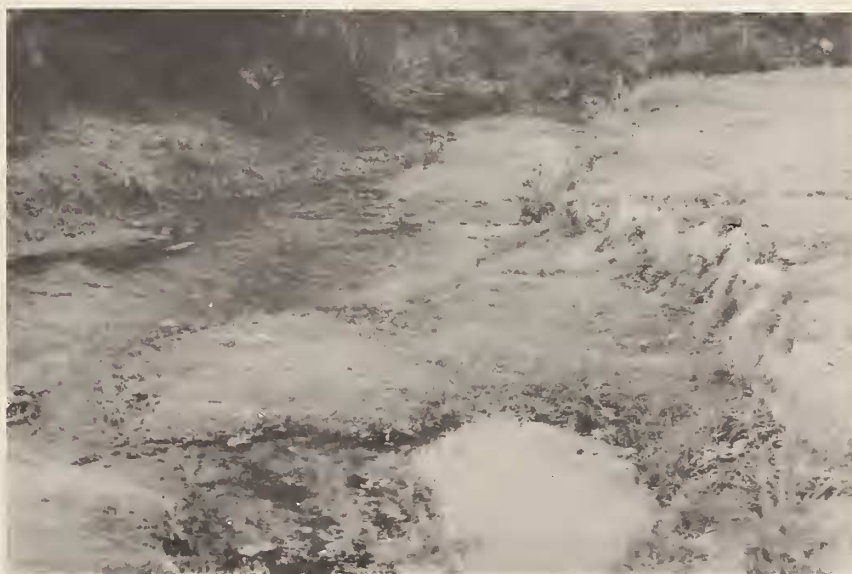


Figure 10

TL *Nymphophilus minckleyi* TAYLOR, gen. et spec. nov.

* *Physa virgata* GOULD

12. Río Salado de los Nadadores at El Cariño de la Montaña, 20 km east of Cuatro Ciénegas. The locality is on the main road from Monclova to Cuatro Ciénegas where the river (here nearly at its head) is narrowly hemmed by the mountain ridge forming the eastern edge of the valley of Cuatro Ciénegas. Mollusks were collected from within a radius of about 4 m, in a spring beside the river and in a protected spot along the edge of the stream (Plate 12, Fig. 10). The spring forms a pool about 6 m long, with a bottom of fine sand and silt overlain by algae and with scattered *Potamogeton*. *Cochliopina* and *Pisidium* were sparse in the bottom of the pool, *Physa* and *Helisoma* common. Along the edge of the stream, in fine mud among watercress, *Cochliopina* and *Pisidium* were common. D. W. Taylor, 12-IV-1965.

Pisidium compressum PRIME

Cochliopina riograndensis (PILSBRY & FERRISS)

Gundlachia excentrica (MORELET)

Helisoma anceps (MENKE)

Physa virgata GOULD

SYSTEMATIC DISCUSSION

Previous Work

Virtually no freshwater mollusks have been collected previously in the arid interior of northern México, the Altiplanicie Septentrional. The indispensable summary by VON MARTENS (1890-1901) lists only 1 from Coahuila. I have been able to find only 5 published records from the state: *Lampsilis salinasensis* SIMPSON (in DALL, 1908); *Frier-sonia iridella* (PILSBRY & FRIERSON) (DRAKE, 1951); *Limnaea desidiosa* SAY (PILSBRY, 1904); *Physa osculans rhyssa* PILSBRY (1899c); and *Physa berendti* DUNKER (DALL, 1905). Edward Palmer, of the U.S. Department of Agriculture, traveled extensively in México in collecting plants. According to DALL (1905:193) he "collected a considerable number" of mollusks that have not been recorded; perhaps other material from Coahuila is among that in the U.S. National Museum collections. Another record from Coahuila (*Sphaerium transversum*) has been added from University of Michigan collections.

The following abbreviations have been used:

- M. Monotypy
- O.D. Original designation
- S.D. Subsequent designation
- UMMZ University of Michigan Museum of Zoology
- USNM U.S. National Museum

PELECYPODA

SCHIZODONTA

UNIONACEA

ELLIPTIONIDAE

The basic reference to freshwater mussels is the catalogue by SIMPSON (1914). This work gives descriptions and general ranges of all species, but the classification has been modified subsequently. Studies by ORTMANN (1912 and others) have led to the classification summarized by WALKER (1918), which is the one generally in use in America. Mexican species (not listed by WALKER) have been summarized by FRIERSON (1927). The more finely dividing classification by MODELL (1964), adopted here, includes data on distribution at the generic level.

Lampsilinae

Actinonaias CROSSE & FISCHER, 1894

(*Disconaias*) CROSSE & FISCHER, 1894

The species within the subgenus were listed by FRIERSON (1927), who recognized 8 forms. According to MODELL (1964:95), its distribution is from northeastern México south to northern Guatemala.

Actinonaias (Disconaias) fimbriata (FRIERSON, 1907)

This species has been recorded previously from Coahuila as *Lampsilis salinasensis* SIMPSON (in DALL, 1908), a synonym of *Actinonaias fimbriata* according to PILSBRY (1910c), ORTMANN (1912), SIMPSON (1914), and later writers. The type locality of *L. salinasensis* was given as "Salinas River, Coahuila, México, Nelson and Goldman," but most likely it is the Río Sabinas at Sabinas, Coahuila.

The summary of Nelson and Goldman's expeditions in México (GOLDMAN, 1951) mentions no Salinas River in Coahuila, but records that they spent 10 days at Sabinas, on the Río Sabinas, from May 20 to 31, 1902. DALL (1908:177) specified that the material was collected by Nelson and Goldman in 1898, but during that year they were not in Coahuila at all (GOLDMAN, 1951).

Other localities for the species include Río Valles, San Luis Potosí, the type locality; Playa de Misantla, Vera Cruz (MARTENS, 1890-1901, pl. 37, fig. 3, reidentified by FRIERSON, 1927); and Río San Juan, Vera Cruz (H. B. BAKER, 1922:20, as *Actinonaias walkeri*, a synonym of *A. fimbriata* according to FRIERSON, 1927).

Frier-sonia ORTMANN, 1912

Frier-sonia iridella (PILSBRY & FRIERSON, 1908)

This species has been found living only in the Río Pánuco drainage of San Luis Potosí (PILSBRY, 1910c), but DRAKE (1951) recorded it from an archeological site, C68, in Coahuila. The location of the cave on the eastern edge of the Cuatro Ciénegas basin has been recorded by GILMORE (1947). This clam cannot surely be considered

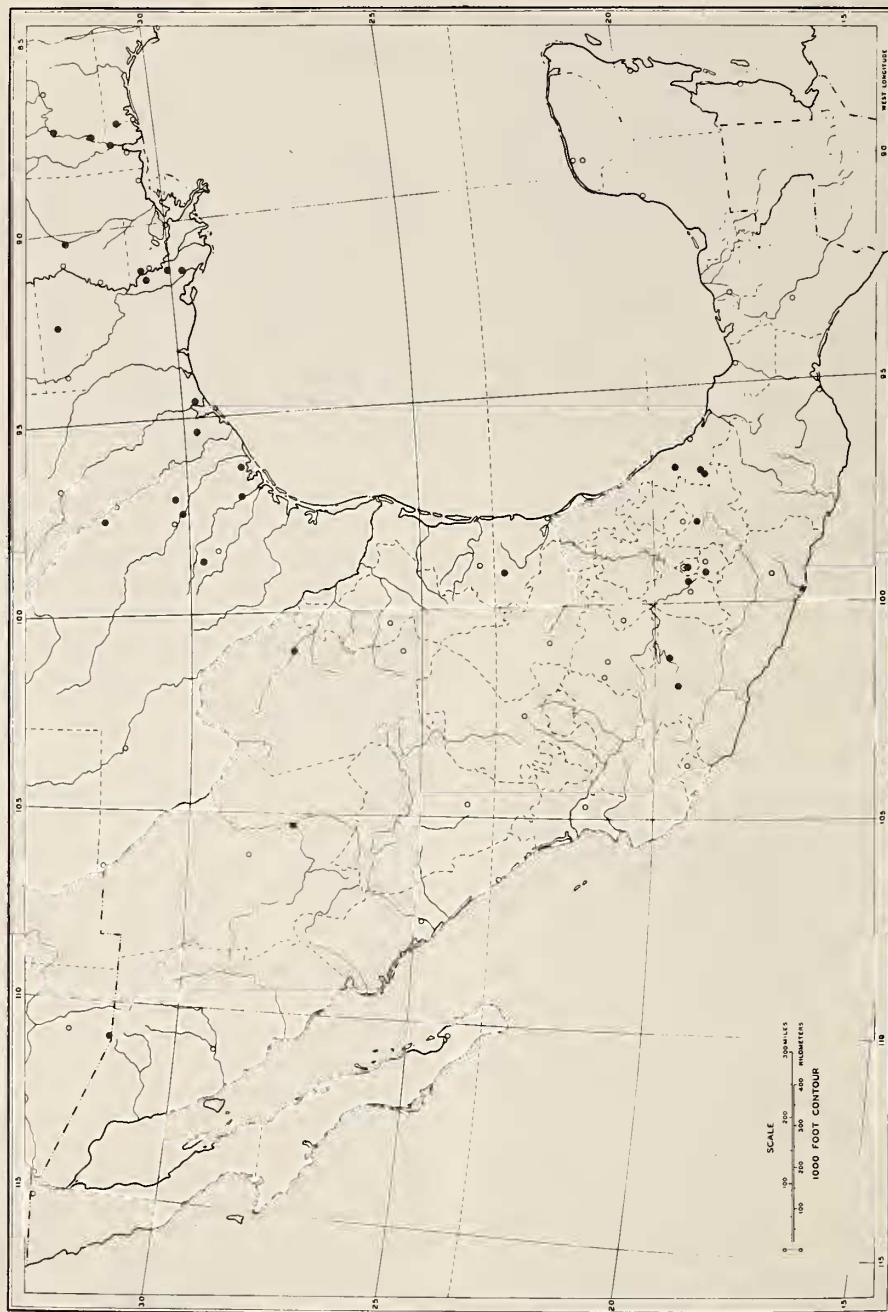


Figure 3

Distribution of *Sphaerium transversum* (Say) in México and southern United States.

part of the modern local fauna without verification, since the shells might have been carried some distance by the Indians.

HETERODONTA

CORBICULACEA

SPHAERIIDAE

The most recent review of this group in North America is by HERRINGTON (1962), whose work provides taxonomic revision, entrance to the literature, and data of general geographic distribution. HEARD (1966) summarized some later modifications in the classification of *Pisidium*.

Sphaerium SCOPOLI, 1777

Sphaerium transversum (SAY, 1829)

In North America this species is found widely east of the continental divide, from Canada southward to central México. Specimens in the University of Michigan Museum of Zoology come from the following localities in northeastern México:

CHIHUAHUA. Slough into Río Conchos (no more precise data); R. J. Drake, 12-VIII-1947 (UMMZ 199895).

COAHUILA. Río Sabinas, Sabinas; Leslie Hubricht, 6-III-1955 (UMMZ 199290).

TAMAULIPAS. Lake at Joya de Salas, 14 miles northwest of Gómez Farías; Rez Darnell, 10-IV-1951 (UMMZ 191838).

The distribution map (Text fig. 3) has been compiled from published records and specimens examined personally. Occurrences in México are based on collections of the U.S. National Museum, University of Michigan Museum of Zoology, and records by MARTENS (1890-1901) and PILSBRY (1904). The record in Arizona is from TAYLOR (1966b); and those elsewhere in the United States from HEARD (1963). The map shows how far the newly reported occurrences in northern México go towards filling in the gap between central México and Texas.

Pisidium C. PFEIFFER, 1821

(*Rivulina*) CLESSIN, 1873

Pisidium (Rivulina) compressum PRIME, 1851

This small clam is one of the most widespread freshwater mollusks in North America, found from Alaska to México. Specimens in the University of Michigan Museum of Zoology come from the following localities in northeastern México:

CHIHUAHUA. Saltales; R. J. Drake, 21-IV-1948 (UMMZ 199523). Laguna Toronto; R. J. Drake, 6-X-1947 (UMMZ 199521).

COAHUILA. Río Salado de los Nadadores, El Cariño, 20 km east of Cuatro Ciénegas; D. W. Taylor, 12-IV-1965 (UMMZ 220144).

TAMAULIPAS. Lake at Joya de Salas, 14 miles northwest of Gómez Farías; Rez Darnell, 10-IV-1951 (UMMZ 199550).

The adult specimens from Coahuila are typical, with coarse striae and a dull shell. The half-grown ones associated are less typical in having few coarse striae, mostly fine striae, broader beaks than commonly found in the species, and a less dull shell. Features of the hinge and outline are so similar that no separation is warranted, and the differences from usual *Pisidium compressum* can be attributed to habitat or to variation toward the southern limit of range of the species. H. B. Herrington corroborated the identification of the species.

GASTROPODA

MESOGASTROPODA

RISSEOACEA

HYDROBIIDAE

Study of the hydrobiid snails from the valley of Cuatro Ciénegas soon revealed the paltry knowledge of this family. Although the species of *Mexipyrghus* seem clearly related to *Tryonia* and *Pyrgophorus*, and fall within the framework of previous classification, the other genera (*Coahuilix*, *Mexithauma*, *Nymphophilus*, *Paludiscala*) do not. The most recent summary of Hydrobiidae is that by WENZ (1938-1944); it is mainly founded on the studies by THIELE (1928). An appraisal of these novel genera from México has thus required not only the compilation of subsequent information, but also the revision and application of new diagnostic characters for many groups within the Hydrobiidae. Accordingly I have reviewed all the freshwater Rissoacea of the Western Hemisphere, and established new diagnoses for the Hydrobiidae and the subfamilies that occur in North America. Tropical American genera that seem to belong in these groups have been so allocated, but the South American groups that are obviously different (for example, *Potamolithus*) are not dealt with at all.

Two large subfamilies that occur in the valley of Cuatro Ciénegas are the Littoridininae and Cochliopinae. Most or all of their species occurring in the Western Hemisphere have been listed, but the other subfamilies have not been dealt with in such detail. A large proportion of the Central American Hydrobiidae cannot be allocated to genus or subfamily on the basis of shell alone. They will remain *incertae sedis* until someone can study them from preserved or preferably living material.

An outgrowth of this and earlier studies of Hydrobiidae is the conclusion that the Bithyniidae are not closely re-

lated, and are more appropriately classified in the Viviparacea. The weighty differences between Hydrobiidae and Bithyniidae have been outlined in the diagnosis and comparisons below: they include features of average body size; operculum (both composition and mode of growth); form of tentacles; pattern of pigmentation; presence of the ciliary feeding apparatus including epitacnia, food-groove, numerous long ctenidial lamellae, and siphon; nuchal lobes; innervation and inferred homology of penis; mode of egg-laying and structure of egg-capsules; shape and structure of fecal pellets; and sperm dimorphism. Classifying the Bithyniidae in the Rissoacea alongside the Hydrobiidae (WENZ, 1938-1944) seems to obscure the relationships of both groups more than it reveals them. Ranking Bithyniidae as a subfamily within Hydrobiidae (THIELE, 1928; MORRISON, 1949) has even less to commend it.

This reclassification of Bithyniidae is of considerable pertinence to the subdivision of Hydrobiidae, for it calls into question the taxonomic value (at this level) of the radula. The classification by THIELE (1928) seems to overemphasize the significance of radular features in Bithyniidae. Similarly it appears that the Delavayidae (classified by Thiele in the Lithoglyphinae of the Hydrobiidae) are more like Cerithiacea than Hydrobiidae, despite some radular features (TAYLOR, 1966a). For these reasons I have not relied on radular characters in diagnosing groups within Hydrobiidae; the correlation of sets of morphological features with details of radular structure will be the surest test of usefulness of the latter. At the level of genus, and often species, the systematic value of the radula has long been established; but at least among the lower Mesogastropoda one may doubt whether the radula shows relationships between families. The acquisition of basal denticles on the central tooth, the modifications in shape and number of cusps, the appearance of glabella and supporting arch, all seem likely to be correlated with similar adaptations in feeding. From a simple radula as in Viviparidae (among the most primitive Mesogastropoda, species of which feed on fine particulate matter by picking it up with the radula, or by a ciliary apparatus), to a more complex radula with interlocking structures and stronger cusps for browsing and rasping, seems likely to be a change that took place independently in several groups.

DIAGNOSIS OF HYDROBIIDAE

The following diagnosis is based on published literature and on personal observations, with profitable influence from discussions with G. M. Davis and W. O. Gregg. It is based mainly on study of American species, but is in-

tended to cover the family as a whole. Characters common to Rissoacea generally have been omitted except to emphasize relationships.

Shell: The shell is minute to small, 1 to 6 mm, rarely over 10 mm. It is planispiral to aciculate, with about 2-8 whorls, coiled dextrally, phaneromphalous to cryptomphalous. The last whorl may be lax; rarely even most of the shell forms a loose corkscrew. The calcareous part of the shell has no color pattern, although the periostracum may. The aperture may be thickened within, or sinuous, or deflected, or flared; but there are no notches, canals, or siphonal grooves. In most genera the shell is smooth except for fine, collabral growth lines; the exceptions are the occurrence of one to a few spiral carinae (as in *Pyrgulopsis* or *Limnothauma*), or blunt calcareous spines (as in *Pyrgophorus*), or low axial ribs or reticulate sculpture (as in *Tryonia*), or fine riblets (as in *Coahuilix*), or numerous spiral cords (as in *Cochliopina* and *Mexithauma*). Elaborate sculpture (except in *Ohrigocca*) and apertural denticulations are unknown. The periostracum is smooth (except for the series of bristles in *Mexithauma*; and in *Potamopyrgus* there may be short periostracal spines on the shoulder, much as in species of *Thiara*). Internally the shell is simple; plications or lamellae are unknown. The apex may be eroded, but is not deciduous, and the tip of the spire is not plugged internally.

Operculum: The operculum is corneous and lacks an internal process or callus; mostly it is paucispiral, rarely multispiral. In a few genera the operculum is in the shape of a hollow cone, with the outer edge of the whorl forming a spiral flange.

Head-foot mass: The foot is strong and mobile, retractile into the shell, truncate in front, rounded behind, with the anterior corners produced into auriculate lobes. There are no tentacles or lobes on its sides or hind end. The only structure associated with mucus glands is an anterior transverse pedal groove, into which the anterior mucus glands empty as in many other families.

The tentacles are filiform, with blunt or rounded tips, mostly circular in cross-section, rarely oval (*Amnicola*). The eyes are usually in discrete swellings on the lateral bases; but may be at the distal end of broad tentacular bases, or sunk into a stout, tapering tentacle with no swelling visible (Lithoglyphinae). Usually the tentacles are symmetrical; in *Clenchiella* the left tentacle is laterally serrate toward the base. Cilia on the tentacles may be evenly distributed, or in discrete tracts, but are vibratile and uniform in length (except *Hydrobia*).

Radula: The central tooth has 1-4 basal denticles on each side.

Pigmentation: Pigmentation is due to a suffusion of fine melanin granules that may give a color ranging from pale

gray through dark gray to purplish, depending on intensity. Only melanin is known, except in *Lithoglyphinae*, which also have larger yellow pigment granules. On the external head-foot the pattern of coloration is usually in bold, diffuse-edged shapes; the tentacles may have short, transverse bars of melanin. White or yellowish hyaline granules are concentrated behind and medial to the eyes, giving the appearance of eyebrows, or rarely distal to the eyes. A few genera, mainly those of subterranean habitat, lack all pigment.

Mantle and cavity: The mantle border is smooth (except that *Mexithauma* has low swellings); a pallial tentacle is unknown (except *Hydrobia*), and no siphons are present. The floor of the mantle cavity is smooth, lacking epitaenia and food-groove. Both ctenidium (formed of about 10-60 triangular lamellae) and osphradium are present. The male reproductive organ is attached to the floor of the mantle cavity; the attachment varies from a little to the left of the mid-line to a sagittal plane through the base of the right tentacle. This organ, the verge, may be a simple penis as in marine *Rissoacea*, but more often it has large accessory glandular processes, and may have 1 or 2 ducts in addition to the vas deferens. The tip of the verge may or may not be ciliated more strongly than the rest. The oviduct courses parallel to the rectum and opens beside it (except in *Mexithauma*).

Reproduction: Hydrobiidae are rarely parthenogenetic (*Potamopyrgus jenkinsi*), sometimes ovoviviparous, and usually oviparous. A free veliger stage is known only in *Hydrobia ulvae*. The eggs are laid singly in capsules, either appressed to some firm surface or loose in the substratum (except *Hydrobia ulvae*, which lays several eggs per capsule).

Habitat: Nearly all Hydrobiidae are freshwater snails. Some are brackish-water, none strictly marine. The rare terrestrial species are all in the Pomatiopsinae.

Fecal pellets: Fecal pellets of Hydrobiidae are as in typical *Rissoacea*. They are elliptical in plan, circular in cross-section, about 2 to 2½ times as long as wide, and non-spiral. No regular arrangement of constituent matter, nor marks of a typhlosole, are evident.

Feeding: All Hydrobiidae are browsers. They may select fine particulate matter, or rasp diatoms and other micro-organisms from firm surfaces, or eat small animals that are injured or freshly dead. They do not have a ciliary mechanism for feeding.

Other features: The verge is of pedal origin. Sperm dimorphism is unknown. Fertilization is internal, and copulation seemingly the rule. A crystalline style is known (or presumed) to be present in all species. Spermatozoa are all of 1 type, cupyrene.

Comparison of shell: Many or most Bithyniidae attain a size over 10 mm; their size thus seems to be significant, as it is correlated with other differentia.

The nearly straight or largely uncoiled shells of Caecidae, Ctiloceratidae, and Orygoceratidae have no parallel in Hydrobiidae. *Liobaicalia* (Baicaliidae) is a close parallel to *Ecpomastrum* (Hydrobiidae, Littoridininae) in being coiled loosely like a corkscrew.

Color pattern in the shell differentiates some species of *Pliopholix* (Pliopholygidae) from *Lithoglyphus* (Hydrobiidae) to which they are otherwise similar. The Bithyniidae also lack color pattern, and so differ from other Viviparacea (Viviparidae, Pilidae, Pliopholygidae). Color pattern in marine *Rissoacea* has not been studied, but in the light of my experience should yield useful characters.

An anterior siphonal notch is present in some marine *Rissoacea*; this feature is not known in Hydrobiidae. A posterior siphonal trace can be seen as a depression at the posterior corner of the aperture in some species of *Tylopoema* (Bithyniidae) and *Pliopholix* (Pliopholygidae). This depression is interpreted as a correlative of an exhalant siphon as in *Bithynia*. No Hydrobiidae have exhalant or inhalant siphons.

Sculpture in Hydrobiidae, though generally weak, shows a wide range of variation. On the average, the Micromelaniidae are more elaborately sculptured: reticulate sculpture, axial ribs, and multiple carinae are more common. The similarity in turritiform shape and relatively complex sculpture between Micromelaniidae and some Littoridininae (Hydrobiidae) raises the question whether these features may not be inherited from their common ancestry.

The smooth periostracum is a character that has not been widely used previously, but seems to be useful. *Antroselates* might be the only American hydrobiid with periostracal sculpture, but it was described as lacking basal denticles on the central tooth. The association of these 2 features strengthens my belief that this snail is not hydrobiid and favors the idea the periostracal characters may be more useful than appreciated previously. *Mexithauma*, here referred to the Hydrobiidae, is unique in its spiral series of short bristles of periostracum.

The Truncatellidae characteristically have a shell with the apex broken off, and the opening in the spire plugged. A similar, perhaps homologous, feature is known in Caecidae. The nearest approach in the Hydrobiidae is the progressive filling of the spire to keep pace with erosion.

Comparison of operculum: The Bithyniidae uniformly have a calcareous operculum with paucispiral nucleus and concentric edges. Neither feature is known in Hydrobiidae, but can be duplicated in Viviparacea. Both Viviparidae

and Pilidae have concentric opercula, and in some Pilidae the operculum bears an internal calcareous pad.

Brachypyrulina (Hydrobiidae, Littoridininae) is the only hydrobiid with an internal reinforcement to the operculum; it has an internal, subspiral, corneous thickening. The internal process of the operculum in Rissoiidae, the internal lamellae of Stenothyridae, and the external calcareous pad of some Truncatellidae, have no counterparts in Hydrobiidae.

The remarkable corkscrew-like operculum of some Hydrobiidae appears to be an independent development in otherwise dissimilar groups. It is known in *Rhampophoma* and *Strombopoma* (Littoridininae), and *Gocea* (Cochliopinae; see HADŽIŠČE, 1956a).

Comparison of head-foot mass: The nuchal lobes found in Bithyniidae and other Viviparacea are unknown in Hydrobiidae. A short pedal tentacle, a posteriorly divided foot, and a posterior mucus gland occur in some marine Rissoiidae; none of these are known in Hydrobiidae.

The tentacles are relatively longer, more flexible, and more acute in Bithyniidae than in Hydrobiidae; in this respect they are intermediate between Hydrobiidae and Pilidae, but more like Hydrobiidae than Viviparidae. In some marine Rissoacea (Rissoiidae, Vitrinellidae, Caecidae) there may be a group of stiff, longer bristles on the tips of the tentacles; perhaps these occur in some brackish-water Hydrobiidae, but not in those of fresh water that I have seen. *Pyrgophorus* (Littoridininae) might be the only hydrobiid in which one tentacle is markedly longer than the other, but the observations (GUILDING, 1828) need confirmation. In *Hydrobia* ciliation of the left tentacle may be greater than on the right, and there are both vibratile and non-vibratile cilia (FRETTER & GRAHAM, 1962). These features, together with the short pallial tentacle known only in *Hydrobia* among all Hydrobiidae, link *Hydrobia* to the marine Rissoiidae.

Comparison of radula: *Bithynia* may have more than 4 basal denticles on each side of the central tooth (up to 6), but otherwise the radula is more like that of Hydrobiidae than other groups. In the well-studied Balkan Pyrgulinae (RADOMAN, 1955) the central tooth lacks basal denticles and hence the group is excluded here from the Hydrobiidae, and referred to the Micromelaniidae following HADŽIŠČE (1956b).

Comparison of pigmentation: Pigmentation is a valuable source of characters, but has been rarely studied. Melanin is retained by snails in alcohol, but other features mentioned soon vanish, and therefore must be studied in life.

Pattern of pigmentation in Viviparacea is distinctive: yellow or orange pigment granules occur in discrete or partly fused aggregations that form irregular splotches of color. The pigmentation of Bithyniidae is entirely like

that of Viviparidae and Pilidae, and entirely unlike that of Hydrobiidae. *Lithoglyphus* is the only hydrobiid I have seen that has any pigment other than melanin. Yellow granules occur in its body in the diffusely scattered pattern in which melanin is arranged in other genera.

Comparison of mantle and cavity: An epitaenia and associated food-groove are found in Bithyniidae and Viviparidae; an epitaenia alone in Pilidae. These features in Bithyniidae are functionally correlated with a number of ctenidial leaflets greater than that known in any Hydrobiidae.

A verge with more than 1 duct is known only in Bithyniidae besides Hydrobiidae. The homology of these structures is doubtful, since the innervation is different in the two groups.

At least in part, the glandular accessory processes of the verge in Hydrobiidae of fresh waters may be an ecological adaptation. That they are not entirely so is shown by the genera that have no accessory processes.

In *Mexithauma* the mantle border is not smooth, but papillose; and the oviduct is bent sharply through more than 90° in its final course, opening on the floor of the mantle cavity.

Comparison of reproduction: The eggs of *Bithynia* are laid in 2 or 3 rows, with 1 egg per capsule, each capsule alternating with adjacent ones. The number of capsules in each mass is commonly 10 to several tens; each capsule has a plug in its dorsal surface (FRETTER & GRAHAM, 1962). The deposition of numerous capsules, and the plug in each one, are features unknown in Hydrobiidae. Neither are these features specially like Viviparacea, of which the Viviparidae are ovoviviparous, and the Pilidae lay clutches of spherical calcareous eggs.

Several characters of *Hydrobia ulvae* are more reminiscent of Rissoiidae than of other Hydrobiidae. Such are the free veliger stage, multiple eggs per capsule, brackish-water habitat, and pallial tentacle. Some of these may be associated with adaptation to the habitat, but collectively they suggest this species is an annectant form close to the common ancestry of both Rissoiidae and Hydrobiidae. Though inconvenient to those writing diagnoses, such forms have the valuable function of reminding one that higher classification is often arbitrary.

Comparison of fecal pellets: ARAKAWA (1962, 1963, 1965) has demonstrated a considerable variety of taxonomically useful characters in molluscan feces. Stimulated by his first paper I began to observe representatives of various families and genera as occasion permitted. An unexpected discovery was the strikingly different shape and construction of fecal pellets in Bithyniidae and Hydrobiidae. In Bithyniidae (*Bithynia* and *Parafossarulus*) they are narrowly elongate, cigar-shaped, and of spiral con-

struction. Those of Hydrobiidae are ovoid and non-spiral, reflecting a fundamentally different mode of formation. Fecal pellets of Pilidae and Viviparidae (Viviparacea) that I have examined are likewise built spirally, but are not as elongate. The spiral mode of formation is rarely evident from shape of the pellets. It can be seen by the contrast in color of the constituent particles, but may be obscured by relatively large grains of silt or fine sand. In studying *Bithynia* I found it convenient to let the snails feed on chalk, after which they produced fecal pellets of fine, even texture that were clearly spiral. The fecal pellets of Hydrobiidae I have examined are uniformly elliptical in plan, with bluntly rounded ends and circular cross-section. Genera examined are *Amnicola* (Amnicolinae), *Lithoglyphus* (Lithoglyphinae), *Pomatiopsis* (Pomatiopsinae), *Tryonia* and *Mexipyrus* (Littoridininae), and several Hydrobiinae.

Comparison of feeding: All Bithyniidae studied are able to collect particulate matter with the ctenidium, and pass it along the food-groove to the mouth. The extent to which this is an optional or obligatory mechanism in the family is unknown; but no Hydrobiidae can feed this way. The marine snails that are ciliary feeders are all in groups other than Rissoacea.

Comparison of other features: Few snails are thoroughly known in even gross morphology, so remaining characters are limited by the state of knowledge. Sperm dimorphism is known in Bithyniidae and Viviparidae, but not in Hydrobiidae. The innervation of the penis in *Bithynia* is pallial, a character showing affinity to the Pilidae (Viviparacea), which have a pallial penis.

Genera described as Hydrobiidae here excluded

The genera mentioned below were first described as Hydrobiidae, and are surely closely related to the family. The criteria that seem most useful to me enjoin classification in different families. The gradual accumulation of knowledge will reveal whether the differentia and the ranks of these other groups have continued usefulness.

Antroselates HUBRICHT, 1963, was described as lacking basal denticles on the central tooth of the radula. Accordingly it is not hydrobiid; I suggest it may be an American representative of the Micromelaniidae, Emmericiinae.

Rachipteron THOMPSON, 1964, is most likely one of the Rissoidae in the broad sense of COAN (1964), but might be included in the Stenothyridae even if that group is separated from the Rissoidae. The characters that seem distinctly non-hydrobiid are the lanceolate (rather than broadly rounded) hind end of the foot; and the spine in the tip of the penis. The simple, bifurcate penis and the

numerous spiral cords on the shell are also distinctive, but in themselves would not indicate affinity outside of the Hydrobiidae.

The criteria THOMPSON (1964) used for classifying *Rachipteron* in the Hydrobiidae rather than Rissoidae were the lack of pallial tentacles, and the presence of basal denticles on the central tooth. One of the criteria ANNANDALE & PRASHAD (1921) used to define the Stenothyridae was the presence of basal denticles, and so far as one can tell from their descriptions and illustration they saw no pallial tentacles in the species examined. They did not illustrate the penis but described it as simple, with no lateral process. The foot of the species illustrated is pointed behind. As illustrated by ABBOTT (1951) *Stenothyra* has a verge with no accessory processes, but with a terminal spine; it has a central radular tooth with basal denticles, and lacks pallial tentacles. Obvious differences from *Rachipteron* are the presence of chitinous lamellae on the inside of the operculum, and a posterior pedal tentacle. ABBOTT classified *Stenothyra* in the Rissoidae. While I do not suggest *Rachipteron* is closely related to *Stenothyra*, evidently the two share enough leading features so that they probably belong to the same family; and both are most conveniently excluded from the Hydrobiidae.

Hydrobiinae

Verge with only one duct, the vas deferens (contrast Amnicolinae and Fontigentinae), and with or without accessory processes on the left side that (when present) are glandular and widest at the base (contrast Littoridininae). Eyes in low, discrete swellings on the outer bases of the tentacles (contrast Lithoglyphinae). Pigmentation consists only of melanin; no yellow granules are present in the head-foot (contrast Lithoglyphinae). Operculum corneous, paucispiral (contrast Cochliopinae, Lyogyridae, Nymphophilinae). Shell globose to turritiform, anomphalous to phaneromphalous (contrast Cochliopinae); aperture thickened or thin, but not flared (contrast *Pterides*-group; reproduction ovoviviparous, or eggs laid singly⁷, in smooth capsules with no dorsal laminate crest (contrast Amnicolinae); progression smooth and not step-wise (contrast Pomatiopsinae).

In the present state of knowledge the Hydrobiinae consist of (a) genera similar to *Hydrobia*, and (b) those left over when obviously distinct groups have been separated. The diagnosis is therefore unwieldy, and the group will surely be refined as knowledge increases.

The descriptions and illustrations by MUUS (1963) permit for the first time a comparison of typical *Hydrobia*

⁷ An exception is the brackish-water genus *Hydrobia*; see FRETTER & GRAHAM (1962) and references therein.

with American Hydrobiidae on the basis of several characters. The most similar genus in America seems to be *Marstonia*: it has an elongate, turritiform shell with an acute apex, and a simple verge in which the left lateral accessory process is smaller than in most American fresh-water Hydrobiidae. Other genera close to *Hydrobia* are *Probythinella* (closer to *Hydrobia* than is *Marstonia* in the verge, but with a distinctive truncate shell) and *Fontelicella* (much like *Hydrobia* in shell, but with an elaborate, bulky accessory process). Other genera are progressively less similar to *Hydrobia*, and most of them are so poorly known that they cannot be grouped plausibly. The following list of genera of Hydrobiinae should be taken with this reservation.

Referred genera: On account of the number of groups involved, and the dubious reference of some, virtually no lists of species or summaries of distribution have been compiled. Literature is accessible through the works by F. C. BAKER (1928), E. G. BERRY (1943), and WENZ (1938-1944); more recent papers describing new genera are cited in the bibliography of this paper.

Aroapyrgus H. B. BAKER, 1931 (*Aroa* H. B. BAKER, 1930, non WALKER, 1855).

Birgella F. C. BAKER, 1926

Cincinnatia PILSBRY, 1891

Clappia WALKER, 1909

Fontelicella GREGG & TAYLOR, 1965

Gillia STIMPSON, 1865

Hoyia F. C. BAKER, 1926

Hydrobia HARTMANN, 1821

Marstonia F. C. BAKER, 1926

Notogillia PILSBRY, 1953

Probythinella THIELE, 1928

Pyrghulopsis CALL & PILSBRY, 1886

Somatogyrys GILL, 1863

Walkerilla THIELE, 1928

In reviewing tropical American genera of subfamilies other than Hydrobiinae I had to consult practically all the literature on *Aroapyrgus*, and reviewed that genus along with others. The shell is not distinctive, and probably other species now *incertae sedis* will be included.

Aroapyrgus BAKER, 1931

Aroa BAKER, 1930. Occ. Pap. Mus. Zool. Univ. Mich. 210: 35. Type (O.D.): *Potamopyrgus ernesti vivens* BAKER. Not of WALKER, 1855.

Aroapyrgus BAKER, 1931. Nautilus 44: 143. New name for *Aroa* BAKER.

The following species have been described:

Aroapyrgus alleei MORRISON, 1946. Smithson. Misc. Coll. 106 (6): 14, pl. 2, fig. 4; pl. 3, fig. 3. Allee Stream, Barro Colorado Island, Gatun Lake, Panama Canal Zone.

Aroapyrgus chagresensis MORRISON, 1946. Smithson. Misc. Coll. 106 (6): 14, pl. 2, fig. 3; pl. 3, fig. 4. Río Chagres, near Gatuncilla, Panamá. Also recorded by Morrison from the Río Chagres, near Madronal, Panamá.

Aroapyrgus ernesti (VON MARTENS, 1873) (*Hydrobia*). Festschr. Gesellsch. Naturforsch. Freunde Berlin: 209, pl. 2, fig. 12. Subfossil, Lago de Valencia, Venezuela.

Aroapyrgus globulus (BAKER, 1930) (*Potamopyrgus*). Occ. Pap. Mus. Zool. Univ. Mich. 210: 36, pl. 28, fig. 3. "Venezuela," no precise locality.

Aroapyrgus joseana MORRISON, 1946. Smithson. Misc. Coll. 106 (6): 15, pl. 2, fig. 5; pl. 3, fig. 8. Northern tributary of Río Mata Puerco estuary, San José Island, Archipiélago de las Perlas, Panamá. Also recorded by Morrison from 3 other localities on the same island.

Aroapyrgus latus (HAAS, 1949) (*Potamopyrgus*). An. Inst. Biol. Mex. 20: 312, text-fig. 5. Río Tapajóz, Santarém, bay Mapire, Pará, Brasil. Also recorded by HAAS (1949, 1950, 1952) from several other localities in the lower Amazon valley, Brasil.

Aroapyrgus panamensis (TRYON, 1863) (*Amnicola*). Proc. Acad. Nat. Sci. Philadelphia 15: 146, pl. 1, fig. 6. Panamá (no specific locality). So assigned by Morrison (1946).

Aroapyrgus putealis (BAKER, 1930) (*Potamopyrgus*). Occ. Pap. Mus. Zool. Univ. Mich. 210: 35, pl. 28, figs. 2, 5. Pond a few kilometers above the town of Estación Táchira, near the left bank of Río Lobaterita, state of Táchira, Venezuela.

Aroapyrgus ernesti vivens (BAKER, 1930) (*Potamopyrgus*). Occ. Pap. Mus. Zool. Univ. Mich. 210: 33, pl. 28, figs. 1, 4, 6, 7. Quebrada Vaca, tributary to Quebrada Carabobo, southeast by south from Boquerón, state of Yaracuy, Venezuela. Recorded by Baker from several localities in central and western Venezuela.

BAKER (1930) noted that females reach a larger size than males. Numerous embryonic young were observed in *Aroapyrgus ernesti vivens* and *A. putealis*. The shell is relatively shorter and wider than that of *Pyrghophorus*, and the central tooth of the radula bears 2 instead of 3 basal denticles. The verge is simple, with no accessory glands, arises from inside a circular fold around its base, and originates markedly to the right of the midline rather than in the midline as in *Pyrghophorus*. The distal half of the verge is pigmented, and narrower than the unpigmented proximal half.

This group was established as a subgenus of *Potamopyrgus* (*Pyrghophorus* as used herein) by BAKER, and subsequently raised to generic rank by MORRISON (1946). According to the criteria for subdivision of the Hydrobiidae used herein, *Aroapyrgus* is not even in the same subfamily as *Pyrghophorus*. The origin of the verge from

within a circular fold is unique in Hydrobiidae, and one may wonder whether the genus is properly included in the Hydrobiinae.

Hydrobiinae? *incertae sedis*

(Text figure 4)

Two specimens, each from a different locality, represent a smooth-shelled small species that cannot be assigned to genus on shell characters.

Localities and material examined: Unnamed laguna west of Río Churince; D. W. Taylor, 14-IV-1965 (UMMZ 220157) (figured specimen). Río Mesquites, 9 km SW Cuatro Ciénegas; D. W. Taylor, 13-IV-1965 (UMMZ 220184).

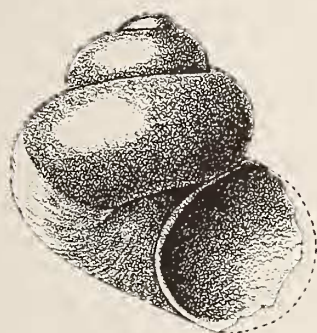


Figure 4

Hydrobiinae, *incertae sedis*. Figured specimen, UMMZ 220157. Length 1.1 mm; width 1.0 mm; 3 whorls.

Amnicolinae TRYON, 1866

Hydrobiidae with a verge including 2 ducts: the vas deferens, and an accessory duct in a lateral appendage on the left. Eggs in single capsules with a dorsal ridge. Operculum corneous, paucispiral. Shell with blunt apex.

Referred genera: *Amnicola* HALDEMAN, 1840 (widely distributed in North America; 3 species).

Marstoniopsis ALTENA, 1936 (northwestern Europe; 1 species).

A group name based on *Amnicola* goes back to TRYON (1862) or GILL (1863); but the scope and relatively narrow definition of this group date only to TRYON (1866).

Amnicola is known mainly by the studies of E. G. BERRY (1943). According to this work only *Amnicola* has egg capsules with a dorsal laminate ridge. The accessory duct has not been described in detail, but as illustrated (E. G. BERRY, 1943, text-fig. 1, 2) it originates in or close to the base of the verge. Only 3 species are surely referable to *Amnicola*:

Amnicola limosa (SAY, 1817), found "from the Atlantic coast as far west as Utah, and from Labrador to Florida" (E. G. BERRY, 1943:23).

Amnicola walkeri PILSBRY, 1898, found in the Great Lakes region. This is probably a junior synonym of *Paludina lustrica* SAY (1821), as discussed previously (TAYLOR, 1960).

Amnicola greggi (PILSBRY, 1935b). This species was described originally as *Hydrobia*, a generic name used for a long time for small Hydrobiidae with no marked shell characters. Observation of living material from the type locality in western Wyoming, and from western Montana and southeastern Idaho, U.S.A., shows that it has the laminate egg capsules, verge with 2 ducts, and other external features of *A. walkeri* of Michigan.

Marstoniopsis ALTENA, 1936

Basteria 1:68. Type (O.D.): *Hydrobia steinii* (VON MARTENS).

KRULL (1935) and ALTENA (1936) have contributed most of what is known about *Marstoniopsis*. FRETTER & GRAHAM (1962: 590-591) evidently referred to *M. steinii* by the name *Bythinella scholtzi*, a synonym according to ALTENA (1936). The species was introduced from continental Europe to England, not from America as stated by FRETTER & GRAHAM. The similarities to the American genus *Marstonia* that ALTENA (1936) pointed out are due to errors by F. C. BAKER (1928). In North America *Amnicola* is markedly distinct in its egg capsules and verge, and it is to this genus that *Marstoniopsis* is clearly similar.

Whether the European genus *Bythinella* should be grouped with *Amnicola* and *Marstoniopsis* is uncertain in the present state of knowledge. As described and illustrated by BREGENZER (1916) and KRULL (1935), the egg capsules are smooth, without a dorsal ridge; the distal end of the accessory process is swollen; and the accessory duct has a far longer and more swollen base than in *Amnicola*. If *Bythinella* is to be added to the Amnicolinae then the diagnosis given above must be modified.

Cochliopinae TAYLOR, new subfamily

Shell trochoid to planispiral, narrowly to broadly umbilicate. Operculum with subcentral nucleus and 3-5 whorls. Rostrum and tentacles with or without 1-2 transverse melanin-pigmented bands. Verge with only 1 duct (vas deferens), with or without 1-2 small accessory processes on the left side. Reproduction ovoviviparous in the 1 genus where known.

Within the Cochliopinae 3 subordinate groups can be recognized that are formalized as tribes (see distribution map, Text figure 5):

Cochliopini, new rank: shell large for the subfamily, minute to medium-sized for the family, generally trochoid with medium-sized to broad umbilicus. Carinae and spiral cords on the shell or color bands in the periostracum may be present. Tropical and warm-temperate America. Referred genera:

Cochliopa STIMPSON, 1865, Panamá (3 species)

Cochliopina MORRISON, 1946, southwestern Texas to Panamá and northwestern Venezuela (20 species)

— *Lacunorbis* YEN, 1950, Pliocene, Nevada, U.S.A. (1 species)

Limnothauma HAAS, 1955a, Lake Titicaca, Perú (1 species)

— *Nanivitreia* THIELE, 1927, Cuba and Jamaica (4 species)

— *Subcochliopa* MORRISON, 1946, Costa Rica and Panamá (3 species)

Horatiini, new tribe: shell minute, planispiral to trochoid, lacking spiral sculpture or color bands; mostly subterranean, found in karst regions. Southeastern North America and southeastern Europe as far east as the Caucasus.

Referred genera:

— *Coahuilix* TAYLOR, gen. nov., Coahuila, México (1 species)

— *Gocea* HADŽIŠČE, 1956a, Lake Ohrid, Yugoslavia-Albania (1 species)

— *Hadziella* KUŠČER, 1932, Yugoslavia (2 species).

Horatia BOURGUIGNAT, 1887, with 3 subgenera besides the typical subgenus:

(*Horatia*) s.s. Yugoslavia and Albania (several species)

(*Daudebardiella*) O. BOETTGER, 1905, Cilicia, Turkey (a few species)

(*Hauftenia*) POLLONERA, 1898, southeastern Europe (8 species, from northeastern Italy and Austria to Dalmatia, Yugoslavia) and southern U.S.A. (2 species in Texas and Alabama)

(*Neohoratia*) SCHÜTT, 1961, southeastern Europe to Caucasus Mts., USSR (about 10 species)

Lyhnia HADŽIŠČE, 1956b, Lake Ohrid, Yugoslavia-Albania (4 species)

Ohridohoratia HADŽIŠČE, 1956b, Lake Ohrid, Yugoslavia-Albania

(*Ohridohoratia*) s.s. (2 species)

(*Ohridohauftenia*) HADŽIŠČE, 1956b (1 species)

Ohriogocea HADŽIŠČE, 1956b, Lake Ohrid, Yugoslavia-Albania

(*Ohriogocea*) s.s. (2 species)

(*Karevia*) HADŽIŠČE, 1956b (3 species)

Clenchiellini, new tribe: shell small, planorboid. Two carinae may be present; spiral cords or color bands are unknown. Northwestern North America (early Tertiary only) and southeastern Asia. One genus:

Clenchiella ABBOTT, 1948 (6 species).

Few morphological data are available for members of this group, so they are tied together by only a few characters. In practically all Hydrobiidae the shell is turritiform to globose and the operculum is paucispiral with its nucleus near the anterior-columellar side. Thus the features of shell and operculum in Cochliopinae are especially distinctive. The black tentacular bands of *Clenchiella* are found in species of *Cochliopa*, *Cochliopina*, and *Subcochliopa*, but the significance of this character is somewhat lessened by similar pigmentation in *Hydrobia*. No such bands occur in any Nearctic Hydrobiidae I have examined.

A particularly distinctive feature of *Clenchiella* is the series of 6-7 low swellings on the proximal posterior border of the left tentacle. This is unique in Hydrobiidae so far as known, but it is like the structure of the marine Caecidae and Vitrinellidae as described by MOORE (1962). The rarity of this tentacular structure alone might suggest the homology of these swellings on the left tentacle. Other characters are common to Cochliopinae and Vitrinellidae, however: a multispiral operculum with subcentral nucleus, and a low trochoid shell with broad umbilicus and strong spiral sculpture. These features are not associated in all species of these groups, but they are common and characteristic. Taken together these features suggest phylogenetic relationship. I suggest that the Vitrinellidae are derived from Cochliopinae of the Hydrobiidae. Such an interpretation, based on morphological grounds, is supported by the fact that *Clenchiella* is one of the few known Hydrobiidae living in brackish water.

Tribe Cochliopini, new rank

This group is the subfamily Cochliopinae of TRYON (1866) for all practical purposes. Species of only 2 genera (*Cochliopa* and *Cochliopina*) were known at that time, but TRYON's differential features included the same characters of shell form used here.

Cochliopa STIMPSON, 1865

Amer. Journ. Conch. 1: 52. Type (O.D.): *Cochliopa rowelli* (TRYON).

The radula of *Cochliopa rowelli* has been described by STIMPSON (1865 a, b) and MORRISON (1946). Pattern of verge and pigmentation of the 3 named species have been illustrated by MORRISON (1946).

The species are all from the Pacific drainage, in the Isthmus of Panamá and Pearl Islands, Panamá.

Cochliopa diazensis MORRISON, 1946. *Smithson. Misc. Coll.* 106 (6): 27, pl. 2, fig. 15; pl. 3, fig. 18. Río Juan Díaz just below Las Sabanas Road bridge, east of Panamá City, Panamá.

Cochliopa joseana MORRISON, 1946. *Smithson. Misc. Coll.* 106 (6): 28, pl. 2, fig. 18; pl. 3, fig. 19. Río Mata Puerco, San José Island, Archipiélago de las Perlas, Panamá.

Cochliopa rowellii (TRYON), 1863b (*Amnicola*). *Proc. Acad. Nat. Sci. Philadelphia* 15: 147, pl. 1, figs. 8-9. The type locality of the species was first published as Clear Lake, Lake County, California, but Rowell, the collector, later asserted it was at Baulinas Bay, Marin County, California (ROWELL, 1906). PILSBRY (1905, 1920), PILSBRY & FERRISS (1906), and MORRISON (1939b) have concluded the type locality is in Panamá; and MORRISON (1946) located it more precisely as the Río Matasnillo immediately east of Panamá City, Panamá.

Cochliopina MORRISON, 1946

Smithson. Misc. Coll. 106 (6): 18. Type (O.D.): *Cochliopina riograndensis* (PILSBRY & FERRISS), 1906.

This genus is one of the few known groups of Hydrobiidae with color pattern in the shell. The feature is common in the genus, although not present in all species, and unknown in other genera of Cochliopinae. The pattern is confined to the periostracum and consists of fine, spiral, continuous brown bands of variable width, usually correlated with spiral ridges of the shell, and sometimes fused to form broad bands.

Ovoviviparity is known in 2 species besides *Cochliopina milleri* TAYLOR, spec. nov. GOODRICH & VAN DER SCHALIE (1937) found 3 young in a specimen of *C. francesae*, and LEONARD & HO (1960b) found 30-50 young per adult *C. riograndensis*.

Previously published morphological data are scanty. The pattern of the verge and pigmentation of the head have been illustrated by MORRISON (1946) in 7 Panamanian species. The operculum was illustrated by MORRISON (1946) for *Cochliopina zetcki*, and by LEONARD & HO (1960b) for *C. riograndensis*. The radula of *C. riograndensis* was illustrated by LEONARD & HO (1960b) for *C. riograndensis*, and that of *C. minor* was formulated by MORRISON (1946).

Twenty nominate forms of *Cochliopina* occur from southwestern Texas, in the Río Grande drainage, southward to Panamá and northwestern Venezuela. "All the northern species, ranging from Texas through México to eastern Guatemala as far as Lake Izabal and the Río Dulce, are found only in river systems draining into the Gulf of México and the Caribbean. In contrast, all the

species known from the southeast corner of Guatemala, southward through Nicaragua, Costa Rica, Panamá, and the Pearl Islands in the Gulf of Panamá, occur only in streams of the Pacific drainage" (MORRISON, 1946:18).

The described forms were mostly listed by MORRISON (1946), but for the sake of a complete summary of the American species of the subfamily they are listed again here.

Cochliopina australis MORRISON, 1946. *Smithson. Misc. Coll.* 106 (6): 23, pl. 2, fig. 13; pl. 3, fig. 14. Musselshell Creek, San José Island, Archipiélago de las Perlas, Panamá.

Cochliopina compacta (PILSBRY, 1910) (*Cochliopa*). *Nautilus* 23: 99, pl. 9, figs. 4-5. Río Choy at the cave, south of Las Palmas, San Luis Potosí, México. So assigned by MORRISON (1946).

Cochliopina dulcensis (MARSHALL, 1920) (*Cochliopa*). *Proc. U. S. Nat. Mus.* 58: 302, pl. 17, figs. 1-3. Río Dulce, Guatemala. So assigned by MORRISON (1946).

Cochliopina extremis MORRISON, 1946. *Smithson. Misc. Coll.* 106 (6): 22, pl. 2, fig. 11; pl. 3, fig. 13. Southern tip of San José Island, Archipiélago de las Perlas, Panamá.

Cochliopina francesae (GOODRICH & VAN DER SCHALIE, 1937) (*Cochliopa*). *Misc. Publ. Mus. Zool. Univ. Mich.* 34: 38, pl. 1, fig. 3. Drainage basin of Río de la Pasión, Dept. Petén and Alta Vera Paz, Guatemala. So assigned by MORRISON (1946).

Cochliopina fraternula MORRISON, 1946. *Smithson. Misc. Coll.* 106 (6): 21, pl. 2, fig. 9; pl. 3, fig. 11. Río Mata Puerco, San José Island, Archipiélago de las Perlas, Panamá.

Cochliopina guatemalensis (MORELET, 1851) (*Valvata*). *Test. Noviss.* 2: 22. Río Michatoya, near Istapa, Guatemala. So assigned by MORRISON (1946).

Cochliopina hinkleyi (PILSBRY, 1920) (*Cochliopa*). *Proc. Acad. Nat. Sci. Philadelphia* 72: 198, text-fig. 4. Lake Izabal near Jocolo, Guatemala. So assigned by MORRISON (1946).

Cochliopina infundibulum (MARTENS, 1899) (*Cochliopa*). *Biol. Centr.-Amer., Moll.*: 429, pl. 23, fig. 3. Guatemala (no precise locality). So assigned by MORRISON (1946), who specified the locality Petén, Guatemala.

Cochliopina izabal (PILSBRY, 1920) (*Cochliopa*). *Proc. Acad. Nat. Sci. Philadelphia* 72: 200, text-fig. 6. Lake Izabal near Jocolo, Guatemala. So assigned by MORRISON (1946).

Cochliopina juradoi MORRISON, 1946. *Smithson. Misc. Coll.* 106 (6): 20, pl. 2, fig. 8; pl. 3, fig. 10. Stream leading to northwest mangrove swamp, San José Island, Archipiélago de las Perlas, Panamá.

Cochliopina kugleri (FORCART, 1948) (*Valvata*). *Verhandl. Naturforsch. Gesellsch. Basel* 59: 50, pl. 1, figs.

6a-d. Distr. Acosta, State of Falcón, Venezuela. I have not seen specimens of this form, but reference to the genus *Cochliopina* seems much more likely than to the similar-looking but remote genus *Valvata*.

Cochliopina minor (PILSBRY, 1920) (*Cochliopa*). Proc. Acad. Nat. Sci. Philadelphia 72: 199, text-fig. 5. Polvon, Nicaragua. So assigned by MORRISON (1946).

Cochliopina navalis MORRISON, 1946. Smithsonian Misc. Coll. 106 (6): 22, pl. 2, fig. 12; pl. 3, fig. 12. Stream tributary to bay on southwestern San José Island, Archipiélago de las Perlas, Panamá.

Cochliopina izabal mutation *perstriata* (PILSBRY, 1920) (*Cochliopa*). Proc. Acad. Nat. Sci. Philadelphia 72: 201, text-fig. 7. Lake Izabal near Jocolo, Guatemala. So assigned by Morrison (1946).

Cochliopina picta (PILSBRY, 1910) (*Cochliopa*). Nautilus 23: 100, pl. 9, figs. 1-2. Río Choy near the ford on the road to Tampamolón, and Río Ganina near Rascón; both San Luis Potosí, México. So assigned by MORRISON (1946).

Cochliopina riograndensis (PILSBRY & FERRISS), 1906 (*Cochliopa*). Proc. Acad. Nat. Sci. Philadelphia 58: 171, pl. 9, figs. 10-13. Drift of Río San Felipe near Río Grande, Val Verde County, Texas. Found from Río Grande southward to Río Pánuco, San Luis Potosí, México (PILSBRY, 1920).

Cochliopina tryoniana (PILSBRY, 1890) (*Cochliopa*). Nautilus 4: 52. Polvon, Nicaragua. So assigned by MORRISON (1946).

Cochliopina wetmorei MORRISON, 1946. Smithsonian Misc. Coll. 106 (6): 24, pl. 2, fig. 16; pl. 3, fig. 15. Río Marina, San José Island, Archipiélago de las Perlas, Panamá.

Cochliopina zeteki MORRISON, 1946. Smithsonian Misc. Coll. 106 (6): 19, pl. 2, fig. 7; pl. 3, figs. 5, 9. Río Juan Díaz, just below Las Sabanas Road bridge, east of Panamá City, Panamá.

Cochliopina riograndensis (PILSBRY & FERRISS, 1906)
On the way to the valley of Cuatro Ciénegas, Coahuila, I found *Cochliopina riograndensis* living at 2 localities, 1 in Texas and the other in Coahuila. To my observations on habitat I have added a list of the localities represented in University of Michigan collections.

LEONARD & HO (1960b) have published the only record of occurrence of the species alive. They found it in Independence Creek, Terrell County, Texas, "... living in relatively sluggish water about six inches deep in the clear, cool, fast-flowing stream. *C. riograndensis* was here restricted to the edge of the stream, and was fairly abundant under cobbles of limestone, logs, and in aquatic vegetation."

In Río Salado de los Nadadores at El Cariño, Coahuila (Plate 12, Fig. 10), *Cochliopina* occurred in both a spring beside the river and in protected situations along the edge of the stream. It was sparse in the mud of the spring-pool,

but common among watercress in the fine mud along the stream border.

A similar habitat beside the Devils River at Bakers Crossing, Val Verde County, Texas, also yielded numerous *Cochliopina*. They were most abundant in the soft mud bottom of a seepage-fed pool, where there was an abundant growth of *Chara* and *Myriophyllum*. *Cochliopina* was also in mud at the edge of the main stream, though scarce, and specimens found here were smaller and with less conspicuous color-banding than in the seepage.

The University of Michigan Museum of Zoology has the following lots of *Cochliopina riograndensis* (PILSBRY & FERRISS).

TEXAS, Val Verde County. Pecos River, 7 miles SE Shumla; Leslie Hubricht, 25-V-1938 (UMMZ 197722). Drift of Pecos River at crossing of U. S. highway 90; Leslie Hubricht, 14-V-1955 (UMMZ 197719). Devils River, Bakers Crossing, 22 miles N Comstock; Leslie Hubricht, 24-V-1938 (UMMZ 197720); D. W. Taylor, 11-IV-1965 (UMMZ 220228). Devils River at crossing of U. S. highway 90; Leslie Hubricht, 12-VI-1955 (UMMZ 195512). Devils River N of Del Rio; Leslie Hubricht, 27-II-1955 (UMMZ 197721).

Kinney County. No specific locality; ex Andrews coll. (UMMZ 91726, 117257); ex J. R. Tomlin coll. (UMMZ 117252).

TAMAULIPAS. Storms ranch, Pano Ayuctla, 5 miles NE Gómez Farías; Rez Darnell, 29-V-1951 (UMMZ 191821), 30-V-1951 (UMMZ 191823). Arroyo Encino, 5 miles NE Gómez Farías; Rez Darnell, 26-V-1951 (UMMZ 191824). Arroyo Encino, above Encino, E of Gómez Farías; Rez Darnell, 23-IV-1951 (UMMZ 191822). Río Sabinas at Pan American highway E of Gómez Farías; Rez Darnell, 25-V-1951 (UMMZ 191826). Rancho Pico de Oro, on Río Sabinas E of Gómez Farías; Rez Darnell, 30-IV-1951 (UMMZ 191825).

COAHUILA. Río Salado de los Nadadores, El Cariño de la Montaña, 20 km E of Cuatro Ciénegas; D. W. Taylor, 12-IV-1965 (UMMZ 220145).

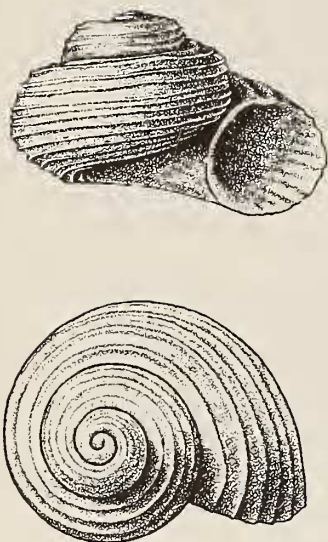
SAN LUIS POTOSÍ. Río Valles, Valles; A. A. Hinkley (UMMZ 28992, 69439, 117251, 117253). Río Ganina, Rascón; A. A. Hinkley (UMMZ 117254).

Cochliopina milleri Taylor, spec. nov.

(Text figures 6, 7; Plate 13, Figures 12, 13)

Diagnosis. Shell about 3 mm in diameter, broadly conical with an abruptly truncate apex, nearly circular whorls, and a broad umbilicus about $\frac{1}{3}$ of the shell diameter. Sculpture consists of about 12-15 spiral cords, covered by dark brown periostracal color bands, that are separated

by approximately equal spaces 4-6 times as wide as the cords.



Figures 6 and 7

Cochliopina milleri TAYLOR, spec. nov. Type, UMMZ 220182.
Length 2.8 mm; width 3.3 mm; $3\frac{1}{2}$ whorls.

Type. UMMZ 220182. Coahuila, México: Río Mesquites at the main road 9 km southwest of Cuatro Ciénegas. D. W. Taylor, 13-IV-1965. Fifty-eight other specimens from the same collection are UMMZ 220183. The species is known only from the type locality (Text figure 2, locality 11).

Comparison and discussion. The most closely similar species are from Guatemala; they are *C. dulcensis* (MARSHALL), from Río Dulce and Lago Izabal; *C. francesae* (GOODRICH & VAN DER SCHALIE), from the drainage of Río de la Pasión; and *C. infundibulum* (MARTENS), of Dept. Petén. These all share with *C. milleri* the distinctive features of a broadly conical shape, whorls roughly circular in cross-section, wide umbilicus, and sculpture of strong spiral cords.

Cochliopina infundibulum differs by its more conical shape, with a more nearly acute apex. A cord on the shoulder of the shell is often conspicuous, but the whorls are not tabulate as in *C. milleri*, and the umbilicus is often but not consistently narrower. No shells with periostracum are available.

Cochliopina dulcensis has fewer and stronger spiral cords than *C. milleri*, and a wider umbilicus and more depressed shape. It is similar to *C. milleri* in its truncate apex, and strong cord on the shoulder of a tabulate whorl. The periostracum on the spiral cords may be more deeply colored than in between, or with no darker color band.

Abundant material of *Cochliopina francesae* is available for comparison, and perhaps for this reason it seems more variable than the other species. It is smaller, usually with an acute rather than truncate apex, and a narrower umbilicus than in *C. milleri*. The strength and spacing of the cords is often as in *C. milleri*, but the shoulder of the whorl may be less pronounced. Color banding is weak or absent. The range of variation is so great that some specimens of *C. francesae* may be indistinguishable from some *C. milleri*. **Habitat.** *Cochliopina milleri* was found only in the Río Mesquites (Plate 11, Figure 8), where it occurred in soft mud in backwaters and protected places along the edge of the stream, associated with *Mexipyrus lugoi* TAYLOR, spec. nov. Unlike the latter, it did not occur also in the main current.

Morphology and biology. All 49 living specimens of *Cochliopina milleri* were females with embryos in the lower part of the pallial oviduct in various stages of development. Evidently males are at least rare in this population, but the extent of collecting is inadequate to indicate parthenogenesis in the species.

Etymology. The species is named in honor of R. R. Miller, University of Michigan Museum of Zoology. The name is doubly appropriate, because of his study of fishes in the Cuatro Ciénegas area; and because one of the most similar species to this new form, *Cochliopina francesae* (GOODRICH & VAN DER SCHALIE), is named for his wife, Frances Hubbs Miller.

Lacunorbis YEN, 1950

Amer. Jour. Sci. 248:187. Type (O. D.): *Lacunorbis nevadensis* YEN.

Explanation of Plate 13

Snails from the Valley of Cuatro Ciénegas, Coahuila.

Photographed by John Tottenham.

Figures 11, 14, 16: *Paludiscala caramba* TAYLOR, gen. et spec. nov.

11. Type, UMMZ 220164. Length 2.5 mm, width 1.2 mm, $7\frac{1}{2}$ whorls.

14. Figured specimen, UMMZ 220165. Length 2.6 mm, width 1.4 mm, $6\frac{3}{4}$ whorls.

16. Figured specimen, UMMZ 220165. Length 2.3 mm, width 0.9 mm, $7\frac{1}{2}$ whorls.

Figures 12, 13: *Cochliopina milleri* TAYLOR, spec. nov.

Type, UMMZ 220182. Length 2.8 mm, width 3.3 mm, $3\frac{1}{2}$ whorls.

Figures 15, 17: *Nymphophilus minckleyi* TAYLOR, gen. et spec. nov.

Type, UMMZ 220188. Length 7.0 mm, width 6.0 mm, $5\frac{3}{4}$ whorls.



Figure 11



Figure 12



Figure 14



Figure 13



Figure 15



Figure 16



Figure 17

Lacunorbis nevadensis YEN, 1950. Amer. Jour. Sci. 248: 187, pl. 1, figs. 7-7b. Pliocene, Truckee Formation, Hot Springs Mountains, Churchill County, Nevada, U.S.A.

Limnothauma HAAS, 1955

Trans. Linn. Soc. London, ser. 3, 1: 302. Type (O. D.): *Limnothauma crawfordi* HAAS.

The anatomy is unknown. The operculum is paucispiral with about $2\frac{1}{2}$ whorls; its apex is subcentral, closer to the center than in most Hydrobiidae but not as close as in some Cochliopinae. A unique feature of the operculum is that it projects over the edges of the aperture and cannot be drawn within. The trochoid shape, broad umbilicus, and basal carination are reminiscent of *Lacunorbis* rather than geographically nearer Cochliopinae.

Limnothauma crawfordi HAAS, 1955. Trans. Linn. Soc. London, ser. 3, 1: 302, text-fig. 28. Isla Titicaca, Lake Titicaca, Perú.

Nanivitreia THIELE, 1927

Zool. Jahrb., Abt. Syst., Ökol. u. Geogr., 53:126. Type (O.D.): *Nanivitreia helicoides* (GUNDLACH).

The broadly conical shell form of *Nanivitreia* is like that of *Cochliopina*, as noted by JAUME & ABBOTT (1948). This resemblance, and the operculum of *N. alcaldei* ("paucispiral but approaching multispiral in appearance, and with approximately 3 or 4 whorls") are features favoring assignment to the Cochliopinae. JAUME & ABBOTT (1948) figured the radula of *N. alcaldei*; no further morphological data on the genus are available.

Nanivitreia alcaldei JAUME & ABBOTT, 1948. Rev. Soc. Malac. "Carlos de la Torre" 6:5, text-fig. 1a-c, 4. Finca de Pollán, Naranjo, Trinidad, Prov. Las Villas, Cuba.

Nanivitreia helicoides (GUNDLACH, 1865) (*Paludinella*). Poey, Repertorio físico y natural de la Isla de Cuba 1:70. Cardenas and Matanzas, Prov. Matanzas, Cuba.

Nanivitreia inconspicua (ADAMS, 1851) (*Valvata*). Contrib. Conch.: 131. Jamaica. So assigned by JAUME & ABBOTT (1948).

Nanivitreia pygmaea (ADAMS, 1849) (*Valvata*). Contrib. Conch.: 42. Jamaica. So assigned by JAUME & ABBOTT (1948).

Subcochliopa MORRISON, 1946

Smithson. Misc. Coll. 106 (6):25. Type (O.D.): *Subcochliopa trochus* MORRISON.

Subcochliopa colabrensis MORRISON, 1946. Smithson. Misc. Coll. 106 (6):26, pl. 2, fig. 14, pl. 3, fig. 16. Río Colabre, Río Bayano drainage, Panamá.

Subcochliopa trochulus (VON MARTENS, 1899) (*Cochliopa*). Biol. Cent.-Amer., Moll.: 429, pl. 23, fig. 2. Río Gran-

de de Terraba at El Pozo, and in marshes of Sierpe, southwestern Costa Rica. So assigned by MORRISON (1946).

Subcochliopa trochus MORRISON, 1946. Smithson. Misc. Coll. 106 (6):25, pl. 2, fig. 17, pl. 3, fig. 20. Río Tribique, Sona, Veraguas Province, Panamá.

Spurious Cochliopini

BURCH (1946) listed 3 species of *Cochliopa* from notes compiled by the late A. M. Strong. Of these species *Cochliopa rowelli* (TRYON) is the type species of *Cochliopa*, and *Cochliopa trochulus* MARTENS is now classified in *Subcochliopa*. The species listed as "*Cochliopa currugata* STEARNS, 1890," from Nicaragua seems to be an error based on the marine snail *Cyclothyca corrugata* (STEARNS), of the family Capulidae.

Cochliopini incertae sedis

"*Planorbis*" *bourguyi* ROXO, 1924. Bol. Brasil Serv. Geol. Mineral. 11:50, fig. E. Pliocene?, Tres Unidos, Prov. Loreto, Perú. Perhaps Cochliopinae.

"*Cochliopa*" *chihuahua* (PILSBRY, 1928) (*Fluminicola*). Proc. Acad. Nat. Sci. Philadelphia 80:116, text-fig. 3. Ojo Caliente, Chihuahua, México. So referred by PILSBRY (1935b).

"*Planorbis*" *pebasana* CONRAD, 1874. Proc. Acad. Nat. Sci. Philadelphia 26:30. Pliocene?, Pebas, or Pichana, or Old Pebas, Prov. Loreto, Perú. Probably Cochliopinae rather than Planorbidae, particularly if the specimens described and illustrated by DE GREVE (1938) represent CONRAD's species.

"*Cochliopa*" *texana* PILSBRY, 1935. Nautilus 48:91, text-figs. 5a-b. Phantom Lake near Toyahvale, Reeves County, Texas. The species is not referable to *Cochliopa* in the strict sense according to MORRISON (1946). The relatively numerous whorls of the operculum and subcentral nucleus (specimens examined in UMMZ collection) show it is one of the Cochliopinae.

"*Planorbis*" sp. DE GREVE, 1938. Abh. Schweiz. Palaeont. Gesellsch. 61:(3):107, pl. 4, figs. 29-30. Pliocene?, Iquitos, Prov. Loreto, Perú. Probably Cochliopinae rather than Planorbidae.

Tribe Horatiini, new tribe

Little biological information about this group is available. Most of the species are known only by shells found in stream-drift from springs or in caves, except for those in and around Lake Ohrid, Yugoslavia-Albania. The planispiral to trochoid shape, and multispiral operculum are both unusual characters in the family that are shared with the Cochliopinae, but the shells are minute, thinner, and lack color pattern. Morphological information on European Horatiini is mainly due to papers by RADOMAN

(1953, 1955a, b). Little is known of any American Horatiini. Comparison is further made difficult because much of Radoman's data concern the nervous system and stomach, completely unknown in American Cochliopinae. Hence the appropriateness of grouping the Horatiini in the Cochliopinae can scarcely be weighed in spite of a substantial body of information.

In the United States *Horatia* is known by 2 nominal forms, *Horatia (Hauffenia) micra* (PILSBRY & FERRISS, 1906) and *H. micra nugax* (PILSBRY & FERRISS, 1906). Both were described from the Guadalupe River, Comal County, Texas, on the limestone-formed Edwards Plateau; PILSBRY (1916) assigned them to *Hauffenia*. The only other published American localities of the group are underground waters at San Marcos, Hays County, Texas; and near Fort Payne, DeKalb County, Alabama (HUBRICHT, 1940).

The distribution of *Horatia* and *Coahuilix* is paralleled by Crustacea of the order Thermosbaenacea (MAGUIRE, 1965), and the cirrolanid isopod *Speocirolana* (COLE & MINCKLEY, 1966).

Coahuilix TAYLOR, gen. nov.

Diagnosis. Shell minute ($1.0 \times 0.5\text{--}0.6$ mm in adults), nearly planispiral, with $2\frac{1}{4}$ whorls, 1 of which is embry-

onic. Right side nearly plane, with a deeply incised suture; left side with an umbilicus about $\frac{1}{3}$ of total diameter. Aperture ovate, $\frac{3}{4}$ as wide as high, flared all around in mature shells. Sculpture consists of raised riblets on the postembryonic shell, irregularly spaced with interspaces 1-5 times the width of the riblets.

Type. *Coahuilix hubbsi* TAYLOR, spec. nov.

Only the type species is included in the genus. It is known only from the type locality, in the valley of Cuatro Ciénegas, Coahuila, México. The riblet-sculpture and apertural flare, especially, set this minute snail off from all other Horatiini.

The name is derived from Coahuila, and the Latin *helix*, *helicis*, feminine, a snail.

Coahuilix hubbsi TAYLOR, spec. nov.

(Text figures 8-13)

Diagnosis. Same as for the genus.

Type. UMMZ 220180. Coahuila, México: from a bottom sample of the northernmost pool of Pozos de la Berra, 14 km southwest of Cuatro Ciénegas. C. L. Hubbs, 6-IV-1961. The same collection yielded 15 other specimens; one is figured (UMZZ 220181), the others unfigured (UMMZ 220177). The locality is number 4 on Text figure 2.

Figure 8

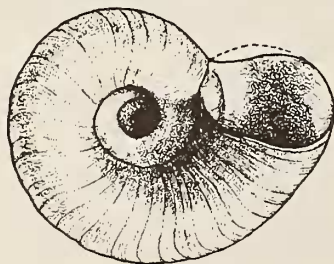


Figure 9

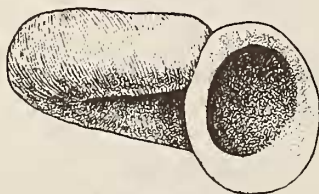


Figure 10

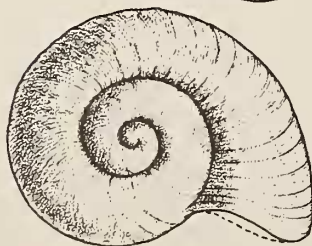


Figure 11

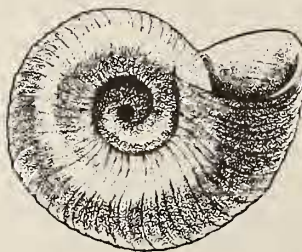


Figure 12

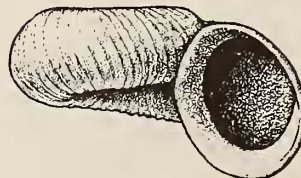
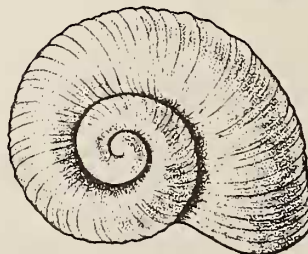


Figure 13



(For explanation see facing page)

Description. The shape of the shell is much like that of a low-spired *Valvata*. The right side is nearly plane, with the outer lip only a little to the left of the plane of the right side of the first whorl; on this side the convex whorls are separated by a deeply incised suture. The whorls are oval in cross-section, and increase in height more rapidly than in width, so that the left side shows a deep umbilicus about $\frac{1}{3}$ the diameter of the shell. The aperture is ovate or almost perfectly elliptical, more than $\frac{3}{4}$ as wide as high, and flared all around in mature shells. The inner lip is simply appressed to the preceding whorl. Sculpture on the postembryonic shell consists of slightly sinuous, irregularly spaced, prosocline riblets separated by spaces 1-5 times as wide.

The 5 mature and unbroken specimens measure as follows (mm):

Width	Height	Width aperture	Height aperture	No. of whorls
1.08	.64	.36	.40	2 $\frac{1}{4}$
1.04	.56	.36	.44	2 $\frac{1}{4}$ r
1.00	.56	.32	.36	2
1.00	.52	.36	.40	2 $\frac{1}{4}$ r
.96	.48	.32	.36	2 $\frac{1}{4}$

r—Type

f—Figured specimen

The 16 specimens are variously preserved, some broken or partly dissolved, others fresh-appearing. These latter seem to retain a nearly colorless periostracum. The strength of the riblets is uniform throughout the length of each riblet, but on some shells the riblets are worn or naturally weak.

The shells are so small that they might have been carried by current from their natural habitat, even from underground. If the relationships of this tiny snail are correctly interpreted, it is the most likely of all known species in the Cuatro Ciéngas area to be subterranean.

Etymology. The species is named in honor of Carl L. Hubbs, Scripps Institution of Oceanography, La Jolla, California.

Tribe *Clenchiellini*, new tribe

Clenchiella ABBOTT, 1948

Carinorbis YEN, 1946. Amer. Jour. Sci. 244: 46. Type (O. D.): *Carinorbis planospiralis* YEN. Not of CONRAD (1862).

Clenchiella ABBOTT, 1948. Nautilus 61: 76. Type (O. D.): *Clenchiella victoriae* ABBOTT.

Carinulorbis YEN, 1949. Jour. Paleont. 23: 573. New name for *Carinorbis* YEN.

Study of numerous early Tertiary fossils from Montana and Wyoming has revealed that most of the specimens

recorded as *Carinulorbis* belong to the Hydrobiidae rather than the Planorbidae, to which YEN referred his genus. The nearly straight growth lines, thicker shell, and large protoconch show these specimens are prosobranchs, not Planorbidae. The shallow suture, with overlapping whorls, and the more flat-walled umbilicus distinguish them from Valvatidae and show they are Cochliopinae. *Clenchiella planospiralis*, type of *Carinorbis*, is especially close to *Clenchiella* and no generic separation seems warranted.

The following species have been described:

Clenchiella microscopica (NEVILL, 1877) (*Valvata*?). Catalogue of Mollusca in the Indian Museum, fasc. E: 21. Port Canning, 24 Parganas District, West Bengal, India. So assigned by ABBOTT (1949).

Clenchiella papuensis JUTTING, 1963. Nova Guinea, Zool., 20: 438, text-figs. 6a-c. Robinson River Plantations near Cloudy Bay, east of Port Moresby, Papua, New Guinea.

Clenchiella planospiralis (YEN, 1946) (*Carinorbis*). Amer. Jour. Sci. 244: 46, pl. 1, figs. 6a-c. Arvada bed, Fort Union Formation, lower Eocene, Sheridan County, Wyoming. Known from the upper part of the Fort Union Formation and lower part of the Wasatch Formation, late Paleocene and earliest Eocene age, Powder River basin, Montana-Wyoming, U.S.A.

Clenchiella sentaniensis JUTTING, 1963. Nova Guinea, Zool., 20: 438, text-figs. 5a-b. Lake Sentani, western New Guinea.

Carinulorbis utahensis LA ROCQUE, 1960. Mem. Geol. Soc. Amer. 78: 38, pl. 3, figs. 23-26. Lower part of Flagstaff Formation, earliest Eocene, Sanpete County, Utah. From examination of the types, and from study of fossils of late Paleocene and Eocene age in Wyoming and Montana, this species is referred to *Valvata*. It is probably a synonym of *V. bicincta* WHITEAVES (1885).

Clenchiella victoriae ABBOTT, 1948. Nautilus 61: 76, pl. 5, figs. 1-7. San Joaquin River 2 miles north of Tanauan, Leyte Island, Republic of the Philippines. Known from one other locality also on the eastern coast of Leyte (ABBOTT, 1948).

MAPEL (1961: 72) recorded "*Carinorbis* sp." and "*Carinulorbis* sp. undet." from the Wasatch Formation in Johnson County, Wyoming. The specimens so identified are referred here to *Valvata*, probably an undescribed species related to *V. bicarinata* LEA. MAPEL's localities are stratigraphically higher than others at which *Clenchiella* has been found.

Figures 8 to 13

Coahuilix hubbsi TAYLOR, gen. et spec. nov.

Figures 8 to 10: Type, UMMZ 220180. Length 0.56 mm; width 1.04 mm; 2 $\frac{1}{4}$ whorls.

Figures 11 to 13: Figured specimen, UMMZ 220181. Length 0.52 mm; width 1.00 mm; 2 $\frac{1}{4}$ whorls.

Fontigentinae TAYLOR, new subfamily

Verge with 3 ducts: vas deferens, and 1 duct in each of 2 accessory processes on the left side of the verge. Operculum corneous, paucispiral.

Referred genera: Only the genus *Fontigens* PILSBRY, 1933, of eastern U.S.A. is included.

This new name is practically a substitute for *Emmericiinae* as used by MORRISON (1949). *Emmericia* lacks basal cusps on the central tooth of the radula, and is considered to belong to the *Micromelaniidae*, as classified by WENZ (1938-1944). The radula of *Fontigens* is similar to that of American *Hydrobiidae*.

Fontigens PILSBRY, 1933

Stimpsonia CLESSIN, 1878. Malak. Blätt. 25: 151. Type (M): *Paludina nickliniana* LEA. Not of GIRARD (1853), nor BATE (1862).

Fontigens PILSBRY, 1933. Nautilus 47: 12. Type (O.D.): *Paludina nickliniana* LEA.

The strikingly distinctive male reproductive system has been described by F. C. BAKER (1928) and E. G. BERRY (1943); the latter has also described and illustrated the radula. The eggs and internal anatomy are unknown.

Lithoglyphinae TAYLOR, new subfamily

Shell globose or conic, 3.5-10 mm long, relatively thick and large for the family. Pigmentation usually consists not only of a dense suffusion of free melanin granules, but also larger yellow-pigment granules in the head-foot mass. The eyes are not in discrete swellings on the outer bases of the tentacles; but either in stout, tapering tentacles; with no swelling or basal peduncle, or on broad, buttress-like bases that are equally stout from the base of the tentacle to the eye. The verge is simple and blade-like, with no accessory glands or processes. The operculum is corneous and paucispiral, as in most *Hydrobiidae*.

Referred genera: *Lithoglyphus* HARTMANN, 1821 (including *Fluminicola* STIMPSON, 1865; *Heathilla* HANNIBAL, 1912; and *Pilsbryus* YEN, 1944).

A group name based on *Lithoglyphus* goes as far back as 1857 when TROSCHER (1856-1893) established a heterogeneous assemblage he called *Lithoglyphi*. TRYON (1866) and P.-H. FISCHER (1880-1887) both recognized a subfamily *Lithoglyphinae*, in each case of different scope but similarly heterogeneous. WENZ (1928) included *Lithoglyphus* by itself in the *Lithoglyphidae*, named but not defined. THIELE'S (1928) composite tribe "Lithoglyphaceae" is essentially WENZ'S (1938-1944) later *Lithoglyphinae*. Even after separating the *Delavayidae* from this assemblage (TAYLOR, 1966a) there is still a mixture of

Hydrobiidae remaining. The only other names based on genera of *Lithoglyphinae* are *Fluminicolinae* CLESSIN (1880), a heterogeneous group; and *Fluminicolidae* HANNIBAL (1912), named but not defined.

Littoridininae TAYLOR, new subfamily

Shell turritiform to elongate-conic; smooth to lirate, plicate, cancellate, or spinose. Operculum corneous; paucispiral and coiled in one plane (except in some aberrant genera of Lake Titicaca, Perú). Verge arising in the midline, or slightly to the right or left of the midline; coiled first posteriorly, or posteriorly and to the right, counter-clockwise through 180 to 360 degrees. Ornament on the verge consists of 2-10 bulbous or elongate lateral lobes, narrower at their attachment; all or some of these are often on the right side. Vas deferens nearly in the midline of the verge, opening through a terminal papilla.

The distinctive verge in this group is known in a small percentage of the American species, so that they seem to form a natural group.

Referred genera (see distribution map, Text fig. 14):

Brachypyrulina HAAS, 1955a. Lake Titicaca, Perú (1 species).

Durangonella MORRISON, 1945. Central México (5 species).

Ecpomastrum HAAS, 1957. Lake Titicaca, Peru (1 species).

Heligmopoma HAAS, 1955a. Lake Titicaca, Peru (1 species).

Idiopyrgus PILSBRY, 1911. Northeastern Brasil (4 species).

Littoridina SOULEYET, 1852. Western and southern South America, from Ecuador and the Lake Titicaca region of Peru southward and eastward to southern Brasil, Patagonia, and Chile (about 60 species).

Littoridinops PILSBRY, 1952. East coast of U.S.A., and Bahamas? (3 species); eastern Mexico? (1 species).

Lyrodes DOERING, 1884. Northeastern Argentina—southeastern Brasil (about 5 species).

Mexipyrgus TAYLOR, gen. nov. Valley of Cuatro Ciénegas, Coahuila, México (6 species).

Pyrghophorus ANCEY, 1888. Islands and margins of the Gulf of Mexico and Caribbean Sea. Early Pliocene—Recent (of 40 nomenclatural units probably only 10-15 are valid species).

Rhamphopoma HAAS, 1955a. Lake Titicaca, Peru (2 species).

Strombopoma HAAS, 1955a. Lake Titicaca and Lagunilla Lagunilla, Peru (2 species).

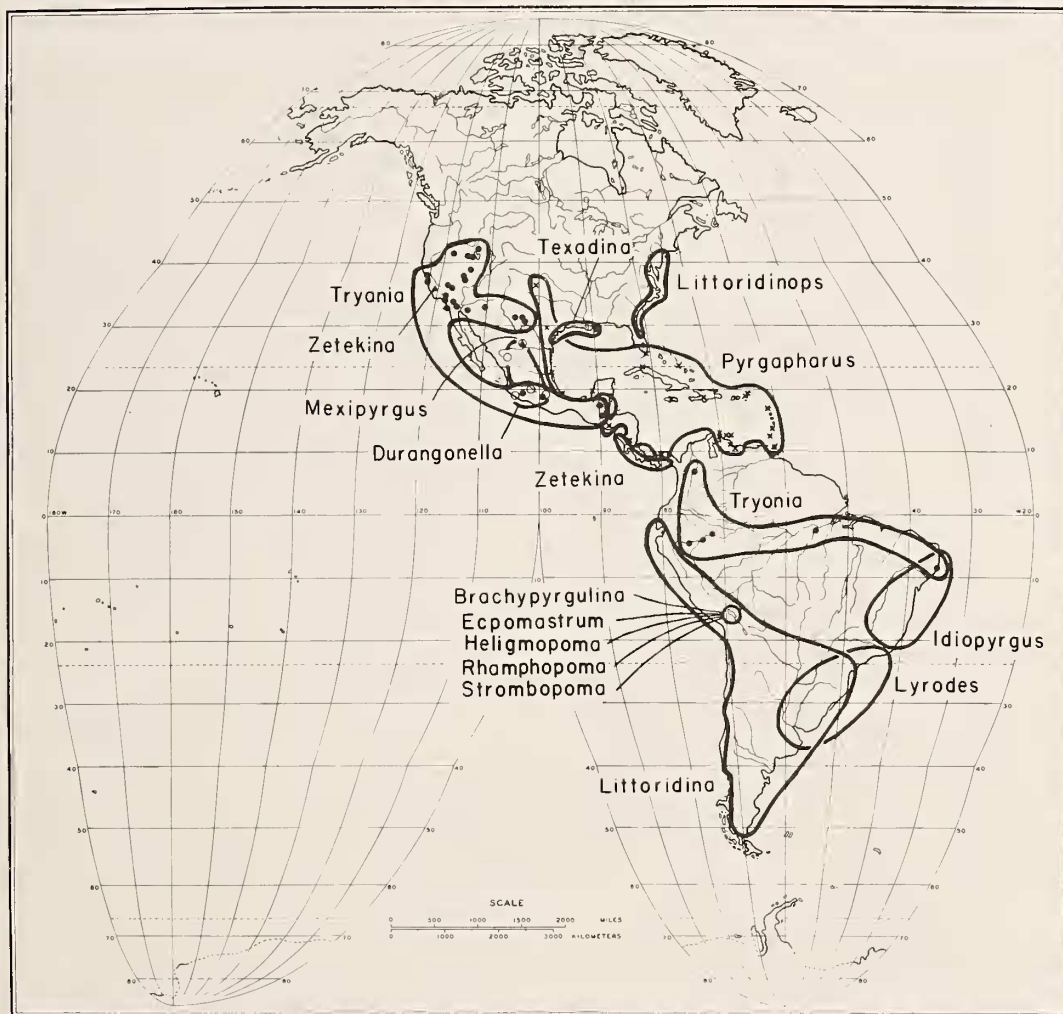


Figure 14

Distribution of subfamily Littoridininae of family Hydrobiidae.

Texadina ABBOTT & LADD, 1951. Southeastern Texas and Louisiana, U.S.A. (1 species).

Tryonia STIMPSON, 1865. Great Basin region of western U.S.A. southward to Guatemala and northeastern Brasil; fossil in Colombia and the upper Amazon region, Brasil-Peru. Late Oligocene or early Miocene to Recent (about 16 species).

Zetekina MORRISON, 1947. Pacific drainage of Nicaragua and Panamá, and Pearl Islands, Panamá (7 species); late Pliocene, California, U.S.A. (1 species).

The Littoridininae as defined here are a taxonomically new group, in that new characters have been used to define it and the scope of the assemblage is novel. Group names have been based on genera included herein, but on different grounds. F. C. Baker (1928: 144) suggested that a family Potamopyrgidae might be warranted for the ovoviviparous, spiny-shelled snails now included in *Potamopyrgus* and *Pyrgophorus*. THIELE (1928) established a tribe Littoridineae in the Hydrobiidae, using features of the radula. This group, raised by WENZ (1939) to subfamily rank, seems heterogeneous when other characters are taken into account.

Subdivision of the Littoridininae is impracticable on account of lack of knowledge. The spinose shell and ovoviviparous reproduction of *Pyrgophorus* and *Potamopyrgus* have been taken to indicate affinity. Yet the verge of *Potamopyrgus* as described by MORRISON (1939a) is simple, unlike the ornamented structure of *Pyrgophorus*; and STIMPSON (1865) and MORRISON (1939a) described the eyes of *Potamopyrgus* as borne on prominent tubercles. These differences indicate the likelihood *Potamopyrgus* is not close to the American forms. In spite of the differences in mode of reproduction, operculum, shell form and sculpture, the American Littoridininae seem a well-knit group according to characters of radula, verge, pigmentation, and relation of eyes to tentacles.

Brachypyrulina HAAS, 1955

Trans. Linn. Soc. London, ser. 3, 1: 301. Type (O. D.): *Brachypyrulina carinifera* HAAS.

The shell is elongate-conic, shorter and broader than that of *Littoridina* and similar to *Heligmopoma* in proportions, but bicarinate. The paucispiral operculum has an internal subspiral corneous callus.

Brachypyrulina carinifera HAAS, 1955. Trans. Linn. Soc. London, ser. 3, 1: 301, text-fig. 27. Lake Titicaca, Perú.

Duragonella MORRISON, 1945

Nautilus 59:18. Type (O. D.): *Duragonella seemani* (FRAUENFELD).

Shell turritiform to aciculate, with 5-8 whorls separated by an incised suture, oval in cross-section. Sculpture consists only of growth lines. The verge has 2 short accessory lobes on the left, toward the distal end.

This group combines characters found in otherwise dissimilar genera. The shell is much like that of smooth species of *Tryonia*, but more elongate and narrow. The verge is more like that of *Zetekina*, a genus with markedly different shell.

Four species have been assigned to *Duragonella* by MORRISON (1945). Localities of these four and a new species described herein are shown on Text figure 15.

Duragonella dugesiana MORRISON, 1945. Nautilus 59:21, pl. 3, fig. 3. Subfossil, "near Andocutira," Michoacán, México.

The index of the American Geographical Society's Map of Hispanic America, 1:1,000,000, lists no place called Andocutira. There is an Andocutin, in the state of Guanajuato near the border of Michoacán, and so this seems most likely to be the type locality.

Duragonella mariae MORRISON, 1945. Nautilus 59:20, pl. 3, fig. 2. Subfossil, dry bed of lake at Tlahuac, 20 km east of Xochimilco, D. F., México.

Duragonella pilsbryi MORRISON, 1945. Nautilus 59:22, pl. 3, fig. 4. Paso del Río, Colima, México.

Duragonella seemani (FRAUENFELD, 1863) (*Hydrobia*). Verhandl. k. k. zool.-bot. Gesellsch. Wien 13: 1025. Durango, México.

Duragonella coahuilae TAYLOR, spec. nov.

(Plate 14, Figures 19, 22)

Diagnosis. Shell 3.0-3.5 mm long, with about 5½ whorls. It differs from the similar *D. mariae* MORRISON by its more nearly circular aperture, more concave columellar lip, less deeply impressed and more slowly descending suture. **Type.** UMMZ 220159. Coahuila, México: Laguna Grande, in the middle of the east side, within about 300 m of the mouth of Río Churince, and about 17 km southwest of Cuatro Ciénegas. D. W. Taylor, 14-IV-1965. Other specimens are UMMZ 220160 (figured specimen) and 220158. The species is known for certain only from Laguna Grande (Text figure 2, locality 10).

Discussion. The specific differences are finely drawn in shells of *Duragonella*, but the known localities are so widely scattered in México (Text figure 2) that they are likely all valid forms. By analogy with the other prosobranch snails from the valley of Cuatro Ciénegas at least 1 species in *Duragonella* would seem to be new. There is no standard by which to judge variation in different pop-

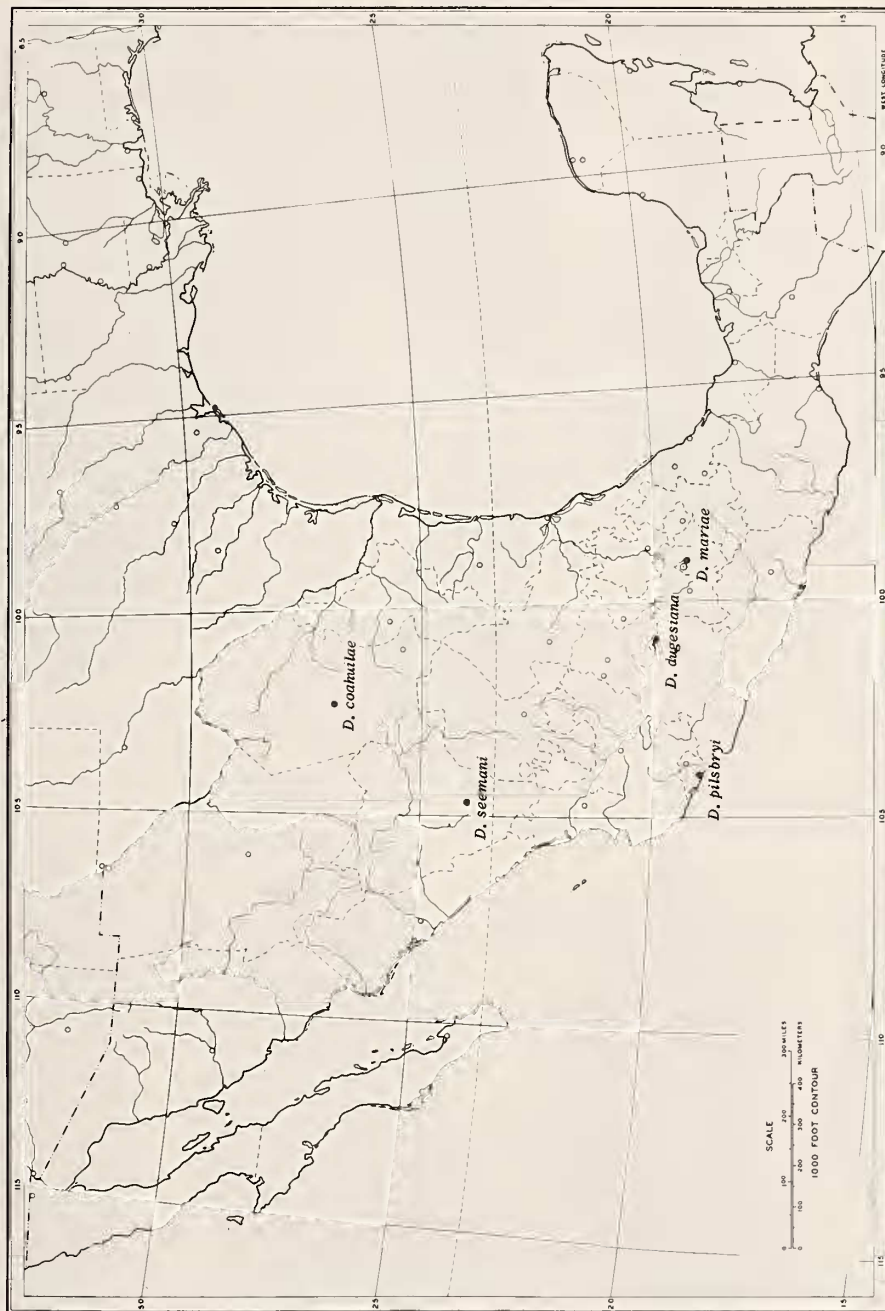


Figure 15
Distribution of *Durangonella*.

ulations of a single species, hence other occurrences of *Durangonella* in the vicinity may or may not represent this species.

Habitat: See p. 164.

Etimology. The species is named for its occurrence in the state of Coahuila.

Durangonella spec.

(Plate 14, Figures 20, 21)

Empty shells of *Durangonella* were found at 2 localities. They probably represent a new species, but I think it is unwise to name another form geographically so close to *D. coahuilae* without knowing more of the range of variation of the species, or trying to collect living specimens. Localities and material examined. Río Mesquites, 9 km SW Cuatro Ciénegas; D. W. Taylor, 13-IV-1965 (UMMZ 220190). Spring tributary to El Mojarral, 1.7 km due east of the northern tip of Sierra de San Marcos, 11 km SW of Cuatro Ciénegas; W. L. Minckley, 13-IV-1965 (UMMZ 220161; 220162, figured specimens).

Durangonella? spec.

Bleached, perhaps subfossil shells that might be *Durangonella* were collected by H. V. Anderson at Laguna de Viesca, Coahuila (USNM, uncatalogued). They might represent part of the fauna of a former lake in that basin.

Ecpomastrum HAAS, 1957

Arch. Molluskenk. 86:137. Type (O. D.): *Ecpomastrum mirum* HAAS.

The loosely coiled, corkscrew-like shell is more like the shells of Littoridininae than those of other Hydrobiidae in South America. The genus is known from only 1 shell, lacking the operculum.

Ecpomastrum mirum HAAS, 1957. Arch. Molluskenk. 86:137, text-figs. 1-2. Lake Titicaca, Peru.

Heligmopoma HAAS, 1955

Trans. Linn. Soc. London, ser. 3, 1: 300. Type (O. D.): *Heligmopoma umbilicatum* HAAS.

The shell is elongate-conic, shorter and broader than that of *Littoridina*. The paucispiral operculum has the edges of its whorls raised as lamellae above the outer surface, though not approaching the extreme of *Strombopoma*.

Heligmopoma umbilicatum HAAS, 1955. Trans. Linn. Soc. London, ser. 3, 1: 300, text-fig. 26. Lake Titicaca, Peru.

Idiopyrgus PILSBRY, 1911

Rep. Princeton Univ. Exped. Patagonia 1896-99 3: 564. Type (O. D.): *Idiopyrgus souleyetianus* PILSBRY.

Hydracme HAAS, 1938. Arch. Molluskenk. 70: 46. Type (O. D.): *Hydracme rudolphi* HAAS.

The narrow, turritiform shell is similar to many other Littoridininae in general shape, but differs by the internally thickened aperture, the anteriorly prolonged outer lip, and the sometimes bisinuate growth line.

Four species have been described; all are from northeastern Brasil.

Idiopyrgus pilsbryi F. BAKER, 1913. Proc. Acad. Nat. Sci. Philadelphia 65: 658, pl. 26, figs. 13-14. North bank of chief affluent of Papary Lake near its mouth, State Rio Grande del Norte, Brasil.

Idiopyrgus rudolphi (HAAS, 1938) (*Hydracme*). Arch. Molluskenk. 70: 46, text-fig. 4. Río São Francisco near Jatobá, State Pernambuco, Brasil.

Idiopyrgus souleyetianus PILSBRY, 1911. Rep. Princeton Univ. Exped. Patagonia 1896-99 3: 565, pl. 41C, figs. 14, 14a; text-fig. 12. Rio Doce, State Espírito Santo, Brasil.

Idiopyrgus walkeri PILSBRY, 1924. Proc. Acad. Nat. Sci. Philadelphia 76:59, text-fig. 9. Rio de Valhas, trib-

Explanation of Plate 14

Snails from the Valley of Cuatro Ciénegas, Coahuila.

Figure 18 by J. Tottenham, others by K. Sakamoto.

Figure 18: *Physa virgata* GOULD. Figured specimen, UMMZ 220217. Length 7.1 mm, width 4.2 mm, $4\frac{1}{4}$ whorls.

Figures 19, 22: *Durangonella coahuilae* TAYLOR, spec. nov. 19. Figured specimen, UMMZ 220160. Length 3.7 mm, width 1.4 mm, 6 whorls.

22. Type, UMMZ 220159. Length 3.3 mm, width 1.4 mm, $5\frac{3}{4}$ whorls. Figures 20, 21: *Durangonella* spec.

25, 26. Figured specimen, male, UMMZ 220203. Length 4.2 mm, width 2.1 mm, $5\frac{1}{2}$ whorls.

20. Figured specimen, UMMZ 220162. Length 4.8 mm, width 1.6 mm, $7\frac{3}{4}$ whorls.

21. Figured specimen, UMMZ 220162. Length 5.9 mm, width 1.8 mm, 9 whorls.

Figures 23 to 26: *Mexipyrgus escobedae* TAYLOR, spec. nov.

23, 24. Type, female, UMMZ 220202. Length 4.5 mm, width 2.5 mm, $5\frac{3}{4}$ whorls.



Figure 18



Figure 19



Figure 20



Figure 21



Figure 22



Figure 23



Figure 24



Figure 25



Figure 26

utary to Rio San Francisco, at Lassance, State Minas Geraes, Brasil.

Hydracme rudolphi HAAS (1938) was based on a series of specimens taken from a fish stomach. A larger series of topotypes, fresh-appearing but rarely retaining the operculum, is catalogued as UMMZ 64012. The variation within this series, and among other lots representing undescribed species from the states Paraiba and Pernambuco, effaces the supposed distinctions between *Hydracme* and *Idiopyrgus*. The sutures may be incised and the whorls convex, but variation is continuous to include a flat-sided spire with scarcely impressed sutures. Details of shape of the aperture also vary from a smaller heavily callused aperture that is straight in profile and inclined slightly to the axis of the shell, to a larger, flared, bisinuate aperture that is less heavily thickened and diverges more from the shell axis.

Littoridina SOULEYET, 1852

EYDOUX, J.F.T., and L.F.A. SOULEYET, Voyage autour du monde . . . sur la corvette La Bonite, 1836-1837, Zoologie, 2: 563. Type (M): *Littoridina gaudichaudii* SOULEYET, 1852.

Heleobia STIMPSON, 1865. Smithson. Misc. Coll. 201: 47. Type (perhaps M.; probably S. D. by PILSBRY, 1911): *Littoridina culminea* (D'ORBIGNY).

The most thorough account of the anatomy of *Littoridina* is that by SOULEYET (1852). Most of the characters he described cannot be evaluated on account of lack of information about other species. *Littoridina gaudichaudii* agrees with the species described by HUBENDICK (1955) in having the eyes on low swellings of the lateral bases of the tentacles; a diffuse pigment pattern with no well defined bands; and oviparous reproduction. It differs in the verge, that has digitate appendages on both sides, an origin to the right of the midline of the body, a vas deferens slightly to the right of the midline in the verge, and the opening of the vas deferens to the left of the terminal papilla. Without knowing the quality of the material studied by SOULEYET (whether living, or preserved in formalin, strongly contracted or not) it is difficult to tell how much reconstruction is included in the drawings. The presence of ornament on the left side of the verge is a real and probably significant difference from the species described by HUBENDICK (1955), but the other differences may be only apparent. So far as the descriptions by IHERING (1895) can be compared, they agree with that of *L. gaudichaudii*.

Subdivision or separation of *Littoridina* will not rest on a firm foundation until at least the gross morphology of many more Recent species is known. Accordingly *Heleobia* is best left as a synonym.

No thorough summary of the South American species of *Littoridina* has been attempted. PILSBRY (1911) brought together all available information through 1909. Later knowledge is due mainly to BIESE (1944, 1947), HAAS (1955a) and HUBENDICK (1955).

Littoridinops PILSBRY, 1952

Nautilus 66: 51. Type (O. D.): *Amnicola tenuipes* COUPER, in HALDEMAN, 1844.

The shell is narrowly elongate, without sculpture except for growth lines, and not significantly distinguishable from shells of *Littoridina*, or even smooth forms of *Pyrgophorus*. The verge differs more from that of *Littoridina* than do those of *Littoridina* and *Pyrgophorus*, so that generic rank seems appropriate. In *L. tenuipes* as described by PILSBRY (1952) there are 5 elongate appendages at the base of the verge on the left side, and about 6 long and several short ones near the tip, on both sides. That species is oviparous.

The known species are found in brackish and fresh water along the east coast of the U. S. A. from New York to Florida; perhaps on Andros Island, Bahamas; perhaps in San Luis Potosí, México.

Littoridinops? blacki (PILSBRY, 1930) (*Hydrobia*). Proc. Acad. Nat. Sci. Philadelphia 82: 301, pl. 22, fig. 4-6. Lake Forsyth, Andros Island, Bahamas. Referred questionably to *Littoridina* by PILSBRY (1950).

Littoridinops? monroensis (FRAUENFELD, 1863) (*Hydrobia*). Verhandl. k. k. zool.-bot. Gesellsch. Wien 13: 1023. Lake Monroe, Florida. Referred questionably to *Littoridina* by PILSBRY (1899).

Littoridinops? tampicoensis (PILSBRY & HINKLEY, 1907) (*Paludestrina*). Nautilus 21: 39, pl. 5, fig. 13. River debris at Tampico, San Luis Potosí, México. Described as related to *L. monroensis*, and not close to other Hydrobiidae of México or Texas.

Littoridinops tenuipes (COUPER), in HALDEMAN, 1844 (*Amnicola*). Monog. limniades, pt. 7, p. 4 of cover. Hope-ton, on Altamaha River 5 miles above Darien, Georgia. PILSBRY (1952) gave the distribution as "Lower Hudson Valley, New York, to Florida."

Lyrodes DOERING, 1884

Bol. Acad. Nac. Ci. Córdoba 7: 461. Type (S. D.): PILSBRY, 1911): *Lyrodes guaranitica* DOERING, 1884.

Both the unity and the rank of the Argentine-Braslian *Lyrodes* are questionable in the lack of anatomical knowledge. The spinose sculpture so common in *Pyrgophorus* (in both fresh and brackish-water habitats) is unknown south of the margins of the Caribbean Sea, so that it is unlikely these groups are congeneric. Possibly *Lyrodes* will

turn out to be a synonym of *Tryonia*, but shells of the latter are generally more narrowly elongate.

Three species of *Lyrodes* from Argentina and southern Brasil were reviewed by PILSBRY (1911), who found 2 embryonic young in a specimen of *L. peteningensis* (GOULD), and 1 in a specimen of *L. scottii* (PILSBRY). More recently named species can be traced through the paper by PARODIZ (1960).

HAAS (1952, 1955b, 1955c), described "*Potamopyrgus*" *subgradatus* from the state of Pará, northeastern Brasil. This might be a *Lyrodes*, if that is a valid group, but cannot be allocated with probability to any genus and is considered here incertae sedis.

Mexipyrgus TAYLOR, gen. nov.

Diagnosis. Shell elongate-conic to turritiform, with conspicuous sexual dimorphism, 4.5-7.2 mm long in adults, anomphalous, with $5\frac{1}{2}$ -7 whorls. Body whorl nearly smooth or with reticulate sculpture; a peripheral keel with nodes usually present at about 3-4 whorls. Periostracum with about 3-20 spiral dark brown bands usually related to surface sculpture. Growth lines prosocyr, with the most distal point below the periphery. Operculum plane, corneous, paucispiral. Verge with a broad, transversely wrinkled base narrowing to a distal, melanin-pigmented bulbous end with a terminal papilla; ornament consisting of 2-3 narrowly pyriform processes, 1-2 on the left side at the distal end and 1 on the right side at $\frac{3}{4}$ of the verge length.

Type. *Mexipyrgus carranzae* TAYLOR, spec. nov.

Distribution. The genus is known only from the valley of Cuatro Ciénegas, central Coahuila, México. Within this area local differentiation is remarkable. The following forms are named herein:

Mexipyrgus carranzae TAYLOR, spec. nov. Laguna Tío Candido.

Mexipyrgus churinceanus TAYLOR, spec. nov. Laguna Churince, Pozos de la Becerra.

Mexipyrgus escobedae TAYLOR, spec. nov. Laguna Escobeda.

Mexipyrgus lugoi TAYLOR, spec. nov. Río Mesquites.

Mexipyrgus mojarrales TAYLOR, spec. nov. West Laguna in El Mojarrales.

Mexipyrgus multilineatus TAYLOR, spec. nov. East Laguna in El Mojarrales.

Etymology. The name is derived from México, and the Greek word *pyrgos*, a tower.

Differentiation within *Mexipyrgus*.

In some ways the discovery of distinct species that are found as single local colonies in the valley of Cuatro Ciénegas is the most interesting aspect of the fauna there.

More study of the known colonies, the search for others, and determining the precise limits of distribution will be necessary for any real advance in knowledge. Yet even at this stage a few observations and inferences are worth while.

The morphological similarities and differences are not correlated consistently with geographic distribution. Some nearby populations (*M. churinceanus* in Laguna Churince and Pozos de la Becerra; *M. lugoi* in Río Mesquites) are generally similar, but others are not (*M. mojarrales* and *M. multilineatus*, within 0.3 km). *Mexipyrgus mojarrales* in El Mojarrales is most like *M. churinceanus*, from the other side of Sierra de San Marcos. The mixtures of similar and different characters found in each species are suggestive evidence that these forms have diverged through the assortment of characters. No one form is likely to have evolved from any other one.

Color banding is rare within the Hydrobiidae, and is unknown in the subfamily Littoridininae except for *Mexipyrgus*. One may well ask whether such a striking feature is not an adaptation, perhaps influenced by predatory fishes. My contribution of knowledge is minor. All *Mexipyrgus* are found within a soft oozy substratum, and are invisible above the surface. There is no chance that the banding is associated with direct visual predation by the fishes, although one cannot exclude a more complicated relationship of color and predation.

Such local species within the genus *Mexipyrgus* lead immediately to a search for isolating mechanisms. More field work will be needed to define the colonies and help establish degrees of relationship, but even from a brief visit it seems that the habitat of this genus is more likely to be discontinuous than that of other snails in the area. *Mexipyrgus* lives in soft flocculent ooze or mud in the lagunas, thus not in the shallows where wave action removes the fine particles. Extensive marshy areas with small streams connecting larger water bodies provide no suitable widespread habitat.

A particularly striking observation on speciation in this group is that none of the colonies differing in shape, sculpture, size, and banding show corresponding differences in the pattern of the verge. Details of ornament (accessory processes, glandular areas, and the like) of the verge are a prolific source of useful characters in this family. In the genus *Fontelicella* (GREGG & TAYLOR, 1965) of the Hydrobiinae, different colonies within 1 species ordinarily show slight differences in pattern of ornament of the verge, and there are always differences in this organ from species to species. From this experience I expected to find, and looked specially for, similarly characteristic patterns of the verge appendages, shape, pigmentation, and the like. Virtually all of the species have a uniform verge; hence I

suspect that the divergence of the various populations of *Mexipyrgus* may have had nothing to do with reproductive isolation, except through geographic separation.

Description of *Mexipyrgus*

Shell. The shell is elongate-conic to turritiform, reaching a maximum size of about 4.5-7.2 mm with $5\frac{1}{2}$ -7 whorls according to the species. Sexual dimorphism is marked, perhaps in correlation with ovoviviparity, so that females are generally more broadly conical than males. Doubtless there are differences in proportions of shell between the various species, but considerable biometric analysis of sexed specimens will be necessary to distinguish the effects of different proportions of males and females, different degrees of dimorphism, and differences between samples of one sex. Diagnoses of the species make practically no mention of proportions of the shell for this reason.

The aperture is elongate-ovate, narrower posteriorly, with a continuous border simply appressed to the preceding whorl. In some adults it may be slightly loosened from the preceding whorl. In profile the outer lip is strongly prosocyr, with the most distal point anterior to the periphery of the whorl. There is no umbilicus.

Sculpture includes both spiral and axial elements. At low magnifications the first whorl appears smooth. Subsequent sculpture begins as a peripheral carina or thread on the second whorl. This carina is usually the dominant element of sculpture for the next 2 whorls, and may persist or disappear thereafter. Other spiral threads may be added subsequent to the peripheral carina. Axial sculpture appears at the second to third whorl as short ribs that form nodes on the spiral carina. The ribs may persist or disappear on the body whorl. The details of ontogeny of sculpture include important criteria for separating species and are mentioned in the diagnoses. In all species the body whorl has a prominent spiral swelling anterior to the suture; this is described as a subsutural cord if narrow, and as a welt if broader and more swollen. This subsutural welt develops in the last 2-3 whorls. Next anterior to the welt is a broad shallow groove, more prominent when the welt is more prominent, bordered anteriorly by a low peripheral cord or an indistinct boundary. This peripheral cord, not always present, is the continuation of the carina of the early whorls.

Color banding of the periostracum varies greatly between species. Frequently there is a broader band, or a group of bands, or a more usually present narrow band on the subsutural welt. Other color bands are often on spiral cords.

Head-foot mass. The foot is truncate in front, broadly rounded behind, with 2 auriculate lobes at the anterior corners that are set off from the posterior parts by shallow

indentations of the sides. The operculigerous lobe is bordered by a shallow, indistinct groove.

The snout is long and tapering, with the buccal mass close to the anterior end. The lips are on the ventro-anterior aspect, and relatively small (about half the area of the anterior end of the snout). They are semicircular to reniform, closer together dorsally, and set off from the snout by a narrow incised groove.

The tentacles are about $\frac{2}{3}$ as high as they are wide, blunt-tipped and not obviously tapering. No discrete ciliary tracts are present; the uniformly distributed cilia are no longer than elsewhere. The eyes lie in the outer bases of the tentacles, in low, indistinct swellings.

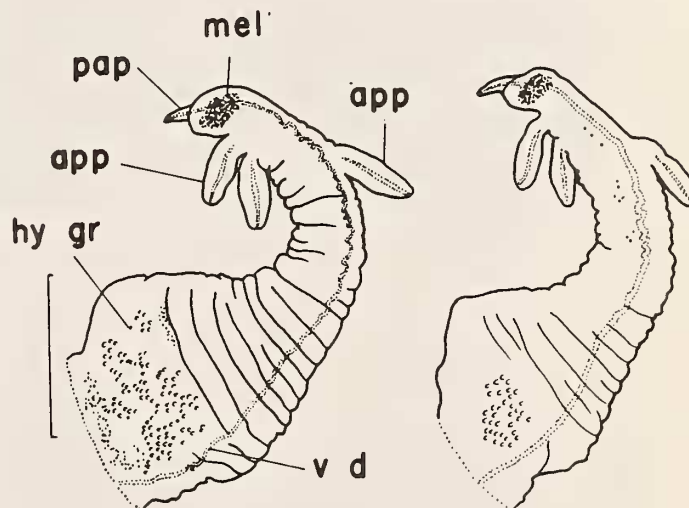


Figure 16

Verges of *Mexipyrgus carranzae* TAYLOR, gen. et spec. nov., dorsal view; scale line = 1 mm. app - appendages; hy gr - hyaline granule; mel - melanin pigment; pap - papilla.

Verge (Text figure 16). The verge has a broad insertion, extending from a little left of the median plane to a little right of a sagittal plane through the base of the right tentacle. It consists of a large penis with 3 elongate appendages, narrower at their attachment than in the middle. An intensely melanin-pigmented area forms a short cylinder within the terminal bulb of the penis. The terminal bulb is heavily ciliated, the cilia being longer there than posteriorly, but the papilla is not ciliated so heavily.

In life the verge is borne curving to the left 90° - 180° , with the long shaft heavily, transversely wrinkled. The appendages are clear, unwrinkled, circular in cross-section, and without ornament. Each has a central lumen opening externally.

Mexipyrus carranzae TAYLOR, spec. nov.

(Plate 15, Figures 27 - 32; Text-figure 16)

Diagnosis. One of the larger species of *Mexipyrus*, attaining a length of 7.0 - 7.2 mm with $6\frac{1}{2}$ - $6\frac{3}{4}$ whorls. A peripheral carina develops on the second or third whorl, and may persist as a dominant spiral element through the fourth whorl. Other relatively strong threads develop on the third and later whorls, and may become as strong as the peripheral cord. A subsutural cord develops on the antepenultimate whorl and becomes a strong cord or even a welt on the body whorl; it is stronger than the peripheral cord. Axial ribs develop on the second or third whorl, and form nodes where they cross the spiral cords. On the body whorl sculpture is cancellate, with the ribs dominant; the numerous spiral cords and fine spiral threads usually weaken or are interrupted as they cross the ribs. The periostracum has 6 - 8 wide brown bands, each on a cord, with a few variable fine bands intercalated. The widest band lies on the subsutural cord; the peripheral band may be but is not always wider than the others. The ground-color of the periostracum varies from light to dark brown, so that the dark brown bands vary in contrast.

Type. UMMZ 220211. Coahuila, México: Laguna Tío Candido, 14 km south of Cuatro Ciénegas. D. W. Taylor, 15 - IV - 1965. Others from the same collection are UMMZ 220212 (figured specimens) and 220213. The species is known only from this laguna (Text figure 2, locality 8).

Comparison. *Mexipyrus carranzae* is like *M. escobedae* in having axial ribs dominant on the body whorl, but the spiral cords are much stronger in *M. carranzae* so that the general pattern is cancellate. It differs further by its larger size, fewer and more distinct bands, by the relatively weaker subsutural cord, and the ontogenetically earlier appearance of the subsutural cord.

Habitat. See p. 163 and Pl. 12, Fig. 9.

Etymology. The name is in reference to Cuatro Ciénegas de Carranza. The town was originally called simply Cuatro Ciénegas, but the name was later lengthened in honor of former President Carranza.

Venustiano Carranza (1859-1920) was born in Cuatro Ciénegas and began his political career as Presidente Municipal, to which office he was elected in 1887 and 1894. He rose to become President of México, 1917-1920.

Pigmentation. The testis appears pink through the shell, when visible, but heavily banded shells may not reveal it. When the shell is broken away the testis can be seen to be brilliant red-orange, in contrast to that of the paler *Mexipyrus escobedae*.

The operculum is darker than in *Mexipyrus escobedae* but details of pigmentation and the attachment of the operculum are nevertheless readily visible through it. White-appearing hyaline granules are more concentrated in the columellar area beneath the operculum than they are in *M. escobedae*. As in that species they are conspicuous by contrast with the black, melanin-pigmented area under the operculum.

In gross external appearance the body appears pale gray except for the dark ventral part of the foot and the black area beneath the operculum. Pigmentation is heavier over-all than in *Mexipyrus escobedae*. Melanin occurs throughout most of the foot, in general deep to the sole, and dominates the white hyaline granules. The skin of the dorsal and dorsolateral surfaces of the snout is lightly dusted with melanin, not clear as in *M. escobedae*. The buccal mass appears pale reddish, and is visible indistinctly. The tentacles lack melanin; their only color is given by a few scattered hyaline granules. The sides of the body-stalk usually lack melanin, so that there are two separate dark areas; one in the area between and just behind the tentacles; the other in the edge of the foot, fading out dorsally. The mantle edge in *M. carranzae* is more heavily pigmented than that of *M. escobedae*, and has a salt-and-pepper appearance due to mixed melanin and hyaline granules.

Hyaline granules in the side of the foot appear yellow in lateral view, from the sole up to behind the tentacles. There is no concentration around the eyes to form "eyebrows," but scattered granules occur in the tentacles.

Mexipyrus churinceanus TAYLOR, spec. nov.

(Plate 16, Figures 33-39; Plate 17, Figures 40-41)

Diagnosis. One of the larger species of *Mexipyrus*, attaining a length of 6.5 - 7.0 mm with 7 whorls. A peripheral carina develops on the second whorl and is the dominant spiral element on the third to fourth whorls; it may persist on the body whorl as an indistinct cord or

Explanation of Plate 15

Mexipyrus carranzae TAYLOR, spec. nov., from the Valley of Cuatro Ciénegas, Coahuila.

Photographed by K. Sakamoto.

27, 28. Figured specimen, male, UMMZ 220212. Length 6.3 mm, width 3.1 mm, $6\frac{3}{4}$ whorls.

29, 32. Type, a female, UMMZ 220211. Length 6.8 mm, width 4.0 mm, $6\frac{3}{4}$ whorls.

30. Figured specimen, a female, UMMZ 220212. Length 7.2 mm, width 3.7 mm, $6\frac{3}{4}$ whorls? (tip eroded).

31. Figured specimen, male, UMMZ 220212. Length 6.6 mm, width 3.3 mm, $6\frac{3}{4}$ whorls? (tip eroded).



Figure 27



Figure 28



Figure 29

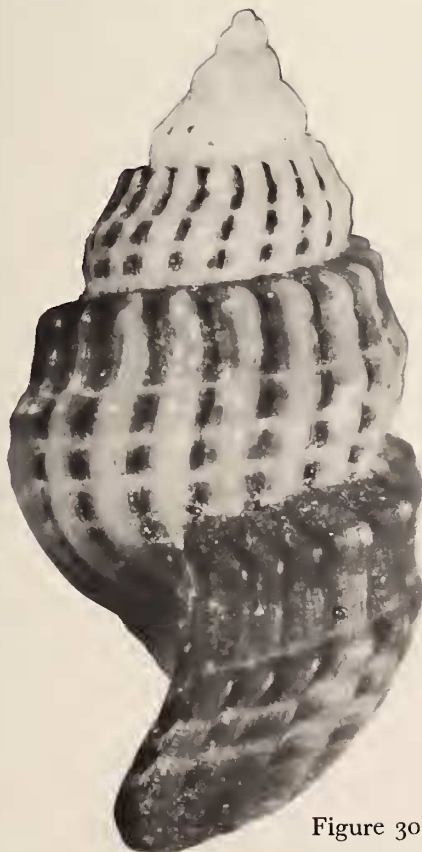


Figure 30



Figure 31

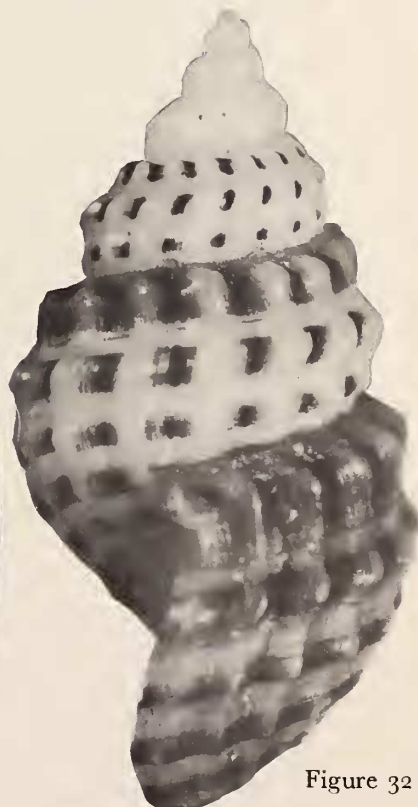


Figure 32

fade before then. A subsutural cord develops on the antepenultimate whorl and strengthens into a welt. Axial ribs developing on the third whorl form nodes where they cross the subsutural cord and peripheral carina, and may persist on the body whorl. On the body whorl spiral sculpture consists of a subsutural welt, variable fine threads, and usually a poorly defined low peripheral cord. Axial sculpture may consist only of growth lines, or well-defined collabral ribs may occur; commonly the ribs are weak and poorly defined, or represented by low nodes on the subsutural welt and the periphery. The periostracum has about 5 - 14 (8 - 10 common) sharply defined wide brown bands of variable spacing; fine bands may be intercalated. The subsutural welt is emphasized by one wide band or a group of nearly fused narrow bands. The periphery bears a band, but not an especially wide one. The ground-color of the periostracum varies from nearly colorless to light brown, so that the bands vary in contrast.

Type. UMMZ 220150. Coahuila, México: Laguna Churince, 16 km southwest of Cuatro Ciénegas. D. W. Taylor, 12 - IV - 1965. Others from the same collection are UMMZ 220151 (figured specimens) and 220149. The locality is number 3 on Text figure 2.

Comparison. *Mexipyrus churinceanus* is most similar in size and banding to *M. lugoi* from the Río Mesquites. It differs in the narrower diameter of the last whorls, so that the whole shell is narrower, the last whorl shorter and narrower, the aperture shorter, and the shell has 1 whorl more at the same length. *M. churinceanus* also has fewer, wider brown bands than in *M. lugoi*, and a subsutural wide band not found in the latter.

In some features of shape, sculpture, and banding *Mexipyrus churinceanus* is like *M. mojarralis* and *M. multilineatus*; the differences are discussed under those species. **Referred specimens.** Not enough well-preserved specimens from Pozos de la Becerra (Fig. 2, locality 4) are available to study in the same detail as the other colonies of *Mexipyrus*. They are at least close to *M. churinceanus* even though showing some differences, and are referred tentatively to that species. Three empty shells retain traces of banding, and show a wide subsutural band with a few others that could be duplicated in *M. churinceanus* from the type locality. These specimens show that in pattern of banding as in shell sculpture the population at Pozos de la Becerra is most like that from Laguna Churince. A few snails with no shell color were collected alive at Laguna Churince, but to judge by the small sample there were many more unbanded shells at Pozos de la Becerra. This population is likely to become extinct in the near future if it is not already, and hence the precise relationship probably will never be determinable. Material examined (all from Pozos de la Becerra): C. L. Hubbs, 6-IV-1961

(UMMZ 220173); W. L. Minckley, 28-XII-1964 (UMMZ 220170); D. W. Taylor, 14-IV-1965 (UMMZ 220167, figured specimens; UMMZ 220166).

Habitat. See p. 162 and Pl. 11, Fig. 7.

Etymology. The species is named for Laguna Churince, the type locality.

Mexipyrus escobedae TAYLOR, spec. nov.

(Plate 14, Figures 23-26)

Diagnosis. One of the smaller species of *Mexipyrus*, attaining a length of 4.5 mm with 5½ whorls. A peripheral carina develops on the second whorl and begins to weaken on the third whorl. Axial ribs developing on the second whorl increase progressively in strength and dominate other sculpture on the body whorl. They cross the peripheral carina to form nodes on the second and third whorls, and bear nodes on the periphery of the body whorl even when the peripheral cord is not present. A subsutural welt develops on the penultimate whorl, and becomes wider than the peripheral cord. On the body whorl the prosocyrte collabral ribs are the dominant sculpture. They are noded along the periphery and on the subsutural welt even when these spiral cords are not continuous. Fine spiral threads are variably developed. The periostracum has 20 - 30 dark brown bands variably fused and mostly indistinct, but the color of the periostracum is darkest on the subsutural welt and along the periphery, or continuously between both. The ground-color of the periostracum is dark, but bands and ground-color are not always distinct.

Type. UMMZ 220202. Coahuila, México: Laguna Escobeda, 12 km south of Cuatro Ciénegas. D. W. Taylor, 15-IV-1965. Others from the same collection are UMMZ 220203 (figured specimen), 220204 (collected alive), and 220205 (empty shells). The species is known only from this laguna (Text figure 2, locality 7). A previous collection by W. L. Minckley, 31-XII-1964, is UMMZ 220208.

Comparison. The dominance of axial ribs on the body whorl distinguishes *M. escobedae* from the other species of the genus. In its heavy pigmentation and strong ribs it is like *M. carranzae* of Laguna Tío Candido, but differs conspicuously by smaller size and much weaker spiral sculpture.

Habitat. See p. 163.

Pigmentation. A series of *Mexipyrus escobedae* survived transport to the laboratory and lived long enough to permit observations on pigmentation and morphology. The features of anatomy that have been studied are mostly included within the description of the genus.

The testis is usually visible as a pale yellow mass within the spire, and thus provides a convenient means for sex

determination. On breaking the shell away from a living snail, one finds the testis is more orange than yellow. This color contrasts with that of the testis in *Mexipyrus caranzae*, which is brilliant red-orange.

When a live snail is withdrawn into its shell the melanin-rich area beneath the operculum appears as a black, roughly semicircular area nearly filling the aperture. The white hyaline granules surrounding the black area are conspicuous in contrast, forming a marginal ring. These features and the attachment of the operculum are readily visible through the thin, nearly colorless operculum. The shell is pale and translucent, so that the black, subopercular area stands in marked contrast to the generally colorless shell and body within.

Extended out of the shell, the snail can be seen to be pale and virtually colorless except for an area of dense melanin pigment in the posterior part of the foot beneath the operculum. This melanin-rich area fades out ventrally toward the sole, and towards the edge of the foot; rarely melanin occurs as a few scattered granules in the anterior $\frac{1}{5}$ of the foot. Elsewhere in the externally visible body melanin occurs regularly only in a short cylindrical mass in the terminal bulb of the verge, and within the mantle edge. It may occur also in the area behind the tentacles in the back of the head as a diffuse scattering of relatively large granules.

Hyaline bodies appear as relatively large, white or translucent granules densely scattered in the edges of the foot, operculigerous lobe, sides of the body stalk, post-tentacular region, and mantle edge. Smaller, white-appearing granules lie in the skin of the snout and provide the only color there except for the buccal mass. They are sparse or absent in a narrow strip along the mid-dorsal length of the snout, so that the buccal mass, salivary glands, and associated musculature can be seen clearly within. These granules are sparsely scattered in the tentacles, but there are no eye-brow-like masses.

Etymology. The species is named for Laguna Escobeda, to which it is restricted.

Mexipyrus lugoi TAYLOR, spec. nov.

(Plate 17, Figures 42-45)

Diagnosis. One of the larger species of *Mexipyrus*, attaining a length of 7.3 mm with 6 whorls. A peripheral carina develops on the second whorl and is the dominant spiral element on the third to fourth whorls; it may persist on the body whorl as an indistinct cord or fade before then. A subsutural cord develops on the penultimate whorl and may strengthen into a welt. Axial ribs developing on the second whorl cross the peripheral carina to form nodes on the second to fourth whorls, but become weaker toward the body whorl. On the body whorl there may be a subsutural welt and a peripheral cord, or spiral sculpture may consist only of a subsutural swelling that is ill-defined. Axial ribs may persist, or be lacking; when present they are usually little more than low nodes on the periphery and subsutural cord. The periostracum has 25 - 35 narrow dark brown bands of roughly equal width separated by roughly equal interspaces. On the subsutural swelling bands may be wider or closer together. The ground-color of the periostracum varies from nearly colorless to light brown, so that the bands vary in contrast.

Type. UMMZ 220185. Coahuila, México: Río Mesquites at the main road 9 km southwest of Cuatro Ciénegas. D. W. Taylor, 13-IV-1965. Others from the same collection are UMMZ 220186 (figured specimens) and 220187. The species is known only from this locality (Text figure 2, Locality 11).

Comparison. *Mexipyrus lugoi* is most similar to *M. churinceanus*. It differs in having a more broadly conical shape, with a broader body whorl and larger aperture; and more numerous and narrower brown bands, with no wide band on the subsutural welt.

Habitat. See p. 164 and Pl. 11, Fig. 8.

Etymology. The species is named in honor of Sr. José Lugo, Jr. of Cuatro Ciénegas, who has aided the study of mollusks and other parts of the remarkable fauna of the

Explanation of Plate 16

Mexipyrus churinceanus TAYLOR, spec. nov., from Río Churince in the Valley of Cuatro Ciénegas, Coahuila.

Photographed by K. Sakamoto.

Figures 33, 34: Type, female, UMMZ 220150. Length 6.2 mm, width 3.1 mm, $6\frac{3}{4}$ whorls.

Figures 35, 39: Figured specimen, female, UMMZ 220151. Length 6.1 mm, width 3.3 mm, $6\frac{3}{4}$ whorls.

Figure 36: Figured specimen, male, UMMZ 220151. Length 5.7 mm, width 2.7 mm, $6\frac{1}{2}$ whorls.

Figures 37, 38: Figured specimen, male, UMMZ 220151. Length 5.3 mm, width 2.6 mm, $6\frac{3}{4}$ whorls.



Figure 33



Figure 34



Figure 35



Figure 36



Figure 37



Figure 38



Figure 39

area by providing field assistance, local facilities, and information about the complex drainage of the area.

Mexipyrus mojarralis TAYLOR, spec. nov.

(Plate 18, Figures 46-49, 51-53)

Diagnosis. One of the smaller species of *Mexipyrus*, attaining a length of 4.5 - 5.0 mm with $5\frac{1}{2}$ - 6 whorls. A peripheral carina develops on the second whorl and persists as such on the third whorl. Axial ribs developing on the second whorl cross the peripheral carina to form nodes on the second and third whorls but do not persist after the third or fourth whorl. A subsutural welt develops on the penultimate whorl and becomes a round-topped cord higher and wider on the body whorl than the peripheral cord. On the body whorl the only axial sculpture is growth lines; spiral sculpture consists of the subsutural and peripheral cords, always present, and of variably developed fine spiral threads. The periostracum has 2 - 4 brown bands, each on a cord. The color band on the subsutural cord is always present; and it is often wider than the others. The ground color of the periostracum is pale yellowish-brown, so that fresh shells are noticeably darker than empty specimens, even aside from the bands.

Type. UMMZ 220192. Coahuila, México: West Laguna in El Mojarral, 1.7 km east-northeast of the northern tip of Sierra de San Marcos. D. W. Taylor, 13-IV-1965. Others from the same collection are UMMZ 220193 (figured specimens) and 220194. The species is known only from this laguna (Text figure 2, locality 5).

Comparison. In shape, sculpture, and color of periostracum *Mexipyrus mojarralis* is similar to *M. churinceanus*, on the other side of Sierra de San Marcos. It shares also with that species the frequent occurrence of a broad color band on the subsutural cord 4 - 5 times as wide as most other bands. *Mexipyrus mojarralis* differs in its smaller size, in the constantly fewer bands of color, in the more sharply defined cords on the body whorl, and in the lack of ribs or rugae on the body whorl.

Mexipyrus mojarralis is found only about 0.3 km from *M. multilineatus*, and one would expect to find them closely similar. Yet they are not as similar to each other as *M. mojarralis* is to *M. churinceanus*. *Mexipyrus mojarralis* is similar to *M. multilineatus* in its relatively small size, and in the lack of ribs or rugae on the last whorls. They also appear at first sight to be similar in having only a few spiral color bands, but this is an artifact of the wear of the shell. *Mexipyrus multilineatus* differs in its paler periostracum, smoother last whorl, numerous narrow color bands, constant absence of a broad subsutural color band, and narrower aperture and shell form.

Habitat. See p. 163 and Plates 9 and 10.

Etymology. The species is named for the area of lagunas and marshes called locally El Mojarral. The name is derived from *mojarra*, the name for the cichlid fishes (*Cichlasoma*) that are common in the lagunas there.

Mexipyrus multilineatus, TAYLOR, spec. nov.

(Plate 18, Figures 50, 54-57)

Diagnosis. One of the smaller species of *Mexipyrus*, attaining a length of 5.0 - 5.1 mm with 6 whorls. A peripheral carina develops on the second whorl and weakens on the penultimate whorl. Axial ribs developing on the second whorl cross the peripheral carina to form nodes on the second and third whorls but do not persist after the third or fourth whorl. A subsutural welt develops on the penultimate whorl and becomes the dominant element of sculpture on the body whorl. On the body whorl the only axial sculpture is growth lines; spiral sculpture consists of a poorly defined subsutural cord, always present, an even more poorly defined, weaker peripheral cord usually present, and variably developed fine spiral threads. The periostracum has 0 - 7 (commonly 2 - 4) narrow brown bands at the beginning of the body whorl; up to about 20 intercalated still narrower bands are often present on the outer lip. The periostracum lacks ground color, so that fresh shells are distinguishable by retaining bands or by a polished surface. The verge has only one accessory process on the left side, unlike other species of the genus. **Type.** UMMZ 220197. Coahuila, México: East Laguna in El Mojarral, 1.9 km east-northeast of the northern tip of Sierra de San Marcos, D. W. Taylor, 13-IV-1965.

Others from the same collection are UMMZ 220198 (figured specimens) and 220199. The species is known only from this laguna (Text figure 2, locality 6).

Comparison. *Mexipyrus multilineatus* is found only about 0.3 km from *M. mojarralis*, but has only a few features like that species (q.v.).

Like *Mexipyrus mojarralis*, *M. multilineatus* shows similarities to *M. churinceanus*, found on the other side of Sierra de San Marcos. As a whole, *M. churinceanus* differs in having a darker periostracum, variably wider brown bands, a frequent broad brown band on the subsutural cord, sometimes axial ribs persistent on the body whorl, and longer shell. Specimens of *M. churinceanus* can be selected that are especially close to *M. multilineatus* in shape, sculpture, and in the occurrence of numerous fine brown bands between the broader ones. These specimens differ in having wider bands, darker periostracum, more numerous broad bands and longer shells.

Habitat. See p. 163.

Etymology. The word *multilineatus* is Latin for many-lined, in reference to a distinctive character of this form.

Pyrgophorus ANCEY, 1888

Bull. Soc. Malac. France 5: 188. Type (S. D.: PILSBRY, 1911): *Pyrgophorus spinosus* (CALL & PILSBRY).

The establishment of this group by Ancey reflected keen insight. The characters he used, the scope of the group, and its relationships seem to have been correctly appraised even in the light of the greater knowledge of today.

The shell is spinose to smooth. When spinose, the spines are calcareous blunt projections from the shoulder of the shell. Smooth shells have shallower sutures, and usually have a more broadly conical form and larger aperture than in smooth *Tryonia*. The strong plicate, cancellate, or lirate sculpture of many forms of *Tryonia* is unknown in *Pyrgophorus*.

Previous reviews of species of *Pyrgophorus* have been published by FISCHER (1860) and ANCEY (1888). The following list is intended to be complete.

Paludina anthracina MIGHELS, 1845. Proc. Boston Soc. Nat. Hist. 2: 22. Tortola. Assigned to *Pyrgophorus coronatus* by MARTENS (1899).

Pyrgophorus coronatus ariomus (CLENCH & AGUAYO, 1937) (*Potamopyrgus*). Mem. Soc. Cubana Hist. Nat. 11: 68, pl. 7, fig. 10. Lake Miragoane, Haiti.

Pyrgophorus coronatus? bermudezi (AGUAYO, 1947) (*Lyrodes*). Rev. Soc. Malac. "Carlos de la Torre" 5: 81, fig. 1-3. Pleistocenc, near Lago Enriquillo, República Dominicana.

Pyrgophorus spinosus brevispira (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 193. Comal Creek, New Braunfels, Comal County, Texas, U.S.A.

Pyrgophorus candeanus (D'ORBIGNY, 1845) (*Paludetrina*). Sagra, Histoire . . . de l'île de Cuba, Mollusques, 2: 9, pl. 10, figs. 13-14. River Madame, Guadeloupe. Assigned to *P. coronatus* by MARTENS (1899).

Pyrgophorus chagresensis (MORRISON, 1946) (*Lyrodes*). Smithson. Misc. Coll. 106 (6): 16, pl. 2, fig. 6, pl. 3,

fig. 6. Chagres River near Gatuncilla, Panamá.

Pyrgophorus cisternicolus (MORELET, 1851) (*Paludina*). Testacea novissima 2: 21. Campeche, State of Campeche, México. Assigned to *P. coronatus* by MARTENS (1899).

Pyrgophorus cisterninus (KÜSTER, 1852) (*Paludina*). Martini and Chemnitz, Syst. Conch.-Cab. 1 (21): 51, pl. 10, figs. 9-10. Bay of Campeche, México; collected by Arthur Morelet.

Pyrgophorus conoideus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 196. Nicaragua.

Pyrgophorus coronatus (PFEIFFER, 1840) (*Paludina*). Arch. Naturgesch. 6 (1): 253. Matanzas, Prov. Matanzas, Cuba is the type locality according to AGUAYO & JAUME (1947).

Pyrgophorus coronatus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 197. Vera Cruz, México. Not of PFEIFFER, 1840.

Pyrgophorus nicaraguanus costuliferus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 195. Nicaragua.

Pyrgophorus crystallinus (PFEIFFER, 1840) (*Paludina*). Arch. Naturgesch. 6 (1): 253. Matanzas, Prov. Matanzas, Cuba, is the type locality according to AGUAYO & JAUME (1947). Assigned to *P. coronatus* by MARTENS (1899).

Pyrgophorus nicaraguanus duplicatus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 195. Nicaragua.

Pyrgophorus candeanus gibbosus (FISCHER, 1860) (*Amnicola*). Jour. Conchyl. 8: 364. Formal name for *Paludina coronata* PFEIFFER, "Var. A" of KÜSTER (1852). Bay of Campeche, México; collected by Arthur Morelet. = *Pyrgophorus cisterninus* (KÜSTER).

Pyrgophorus hibbardi (LEONARD & FRANZEN, 1944) (*Calipyrgula*). Kansas Univ. Sci. Bull. 30: 19, pl. 4, fig. 7. Lower Pliocene, Laverne Formation, Beaver County, Oklahoma, U.S.A.

Pyrgophorus hydrobioides (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 201. Lake Coatpeque, Salvador. Ranked as a distinct species by MARTENS (1899).

Explanation of Plate 17

Mexipyrus from the Valley of Cuatro Ciénegas, Coahuila.

Photographed by K. Sakamoto.

Figure 40, 41: *Mexipyrus churinceanus* TAYLOR, spec. nov. from Pozos de la Becerra

40: Figured specimen, male, UMMZ 220167. Length 5.1 mm, width 2.7 mm, 5 $\frac{3}{4}$ whorls.

41: Figured specimen, female, UMMZ 220167. Length 6.1 mm, width 3.6 mm, 6 whorls.

Figures 42 to 45: *Mexipyrus lugoi* TAYLOR, spec. nov. from Río Mesquites.

42. Figured specimen, female, UMMZ 220186. Length 5.7 mm, width 3.5 mm, 5 $\frac{3}{4}$ whorls.

43. Figured specimen, male, UMMZ 220186. Length 7.8 mm, width 3.8 mm, 7 whorls.

44. Figured specimen, male, UMMZ 220186. Length 5.7 mm, width 3.1 mm, 6 $\frac{1}{2}$ whorls.

45. Type, female, UMMZ 220185. Length 6.8 mm, width 3.9 mm, 6 $\frac{1}{2}$ whorls.



Figure 40



Figure 41



Figure 42



Figure 43



Figure 44



Figure 45

Pyrgophorus candeanus inermis (FISCHER, 1860) (*Amnicola*). Jour. Conchyl. 8: 364. No type locality specified; practically nomen nudum. Assigned to *Pyrgophorus coronatus* by MARTENS (1899).

Paludina jamaicensis ADAMS, 1849. Contr. Conch.: 42. Jamaica. Assigned to *Pyrgophorus parvulus* by BAKER (1924).

Pyrgophorus wrighti minimus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 201. Lake Coatepeque, Salvador.

Pyrgophorus newcombianus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 196. Nicaragua.

Pyrgophorus nicaraguanus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 194. Nicaragua. Assigned to *P. coronatus* by MARTENS (1899).

Pyrgula nicaraguensis NEWCOMB, Ms. Cited by ANCEY (1888) in synonymy of *Pyrgophorus nicaraguanus*. Nomen nudum.

Pyrgophorus wrighti obesus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 201. Lake Coatepeque, Salvador.

Pyrgophorus wrighti oblongus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 200. Lake Coatepeque, Salvador.

Pyrgophorus ornatus (MORELET, 1851) (*Paludina*). Testacea novissima 2: 21. Laguna Coatepeque, Salvador. Assigned to *Pyrgophorus coronatus* by MARTENS (1899).

Pyrgophorus parvulus (GUILDING, 1828) (*Paludina*). Zool. Jour. 3: 537, suppl. pl. 28, fig. 1-3. St. Vincent, Windward Islands, British West Indies. According to BAKER (1924, 1930) the species ranges through Jamaica, Haiti, St. Thomas, St. Vincent, Grenada, Curaçao, Aruba, Bonaire, Klein-Bonaire, and in the Río Yumarito, near Boquerón, State of Yaracuy, Venezuela.

Pyrgophorus wrighti plicatus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 199. Lake Coatepeque, Salvador.

Pyrgophorus productus (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 197. Nicaragua.

Pyrgophorus reevii (FRAUENFELD, 1863) (*Hydrobia*). Verhandl. k.k. zool.-bot. Gesellsch. Wien 13: 1024; 15: 526, pl. 8.

Calipyrgula senta LEONARD & FRANZEN, 1944. Kansas Univ. Sci. Bull. 30: 21, pl. 4, fig. 8. Lower Pliocene, Laverne Formation, Beaver County, Oklahoma. = *Pyrgophorus hibbardi*.

Pyrgophorus spiniferus (ADAMS, 1845) (*Melania*). Proc. Boston Soc. Nat. Hist. 2: 17. Jamaica. Assigned to *P. coronatus* by MARTENS (1899).

Pyrgophorus spinosus (CALL & PILSBRY, 1886) (*Pyrgulopsis*). Proc. Davenport Acad. Nat. Sci. 5: 14, pl. 2, figs.

17-19. Comal Creek, New Braunfels, Comal County, Texas, U.S.A. Assigned to *Pyrgophorus coronatus* by MARTENS (1899).

Bithinia spiralis GUPPY, 1864. Ann. Mag. Nat. Hist., ser. 3, 14: 244. Trinidad. Assigned to *Pyrgophorus parvulus* by BAKER (1930).

Hydrobia texana PILSBRY, 1887. Proc. Davenport Acad. Nat. Sci. 5: 33, pl. 3, figs. 1-6. Guadalupe River and Comal Creek, Comal County, Texas, U.S.A. Referred by PILSBRY (1891) to *Pyrgophorus spinosus*.

Pyrgophorus wrighti transitans (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 200. Lake Coatepeque, Salvador.

Calipyrgula tumida LEONARD & FRANZEN, 1944. Kansas Univ. Sci. Bull. 30: 20, pl. 4, fig. 9. Lower Pliocene, Laverne Formation, Beaver County, Oklahoma, U.S.A. = *Pyrgophorus hibbardi*.

Calipyrgula turricula LEONARD & FRANZEN, 1944. Kansas Univ. Sci. Bull. 30: 20, pl. 4, fig. 4. Lower Pliocene, Laverne Formation, Beaver County, Oklahoma, U.S.A. = *Pyrgophorus hibbardi*.

Pyrgophorus coronatus uncarinatus (VON MARTENS, 1899) (*Amnicola*). Biol. Centr.-Amer., Moll.: 433. Nomen nudum. Reported from Cuba by AGUAYO & JAUME (1947).

Pyrgophorus valenciae (PRESTON, 1909) (*Paludestriana*). Ann. Mag. Nat. Hist., ser. 8, 3: 513, pl. 10, fig. 16. Lago de Valencia, Venezuela. Ranked as a distinct species by BAKER (1930).

Pyrgophorus wrighti (ANCEY, 1888) (*Pyrgulopsis*). Bull. Soc. Malac. France 5: 199. Lake Coatepeque, Salvador. Assigned to *Pyrgophorus coronatus* by MARTENS (1899).

Pyrgophorus zeteki (MORRISON, 1946) (*Lyrodes*). Smithsonian. Misc. Coll. 106 (6): 17, pl. 2, fig. 10. Pedro Miguel, Panama Canal Zone.

Spurious species of *Pyrgophorus*

A number of species have been described by previous authors under the names *Potamopyrgus*, *Pyrgulopsis* or *Lyrodes* and were evidently thought to belong to the group here called *Pyrgophorus*. Virtually all of the spurious forms are assigned herein to *Aroaopyrgus* (Hydrobiinae), or to some genus of Littoridininae, and have been listed under the appropriate category. One species seems to me unlikely to belong even in the Littoridininae: *Lyrodes hertleini* DRAKE (1956), from springs at Las Palomas, Chihuahua, México. If it belongs to an already described group then it might belong to *Fontelicella* GREGG & TAYLOR (1965), but so little is known of Hydrobiidae in the region that one can only speculate.

Rhamphopoma HAAS, 1955

Trans. Linn. Soc. London, ser. 3, 1: 298. Type (O.D.): *Rhamphopoma magnum* HAAS.

The shell is turritiform, as in *Littoridina*. The operculum is ovate in plan along the outer margin, but produced toward the nucleus so that a hollow narrow tube with slight spiral twist projects toward the baso-columellar margin.

Rhamphopoma magnum HAAS, 1955. Trans. Linn. Soc. London, ser. 3, 1: 299, text-fig. 24. Lake Titicaca, Peru.

Rhamphopoma parvum HAAS, 1955. Trans. Linn. Soc. London, ser. 3, 1: 300, text-fig. 25. Lake Titicaca, Peru.

Strombopoma HAAS, 1955

Trans. Linn. Soc. London, ser. 3, 1: 296. Type (O.D.): *Strombopoma ortonii* (PILSBRY).

The shell is turritiform, as in *Littoridina*. The operculum is multispiral, with as many whorls as the shell, conical and hollow, with the edge of each whorl projecting to form a spiral lamella around the outer surface of the cone.

Strombopoma gracile HAAS, 1955. Trans. Linn. Soc. London, ser. 3, 1: 298, text-fig. 23. Lagunilla Lagunilla, basin of Lake Titicaca, Peru.

Strombopoma ortonii (PILSBRY, 1924) (*Littoridina*). Proc. Acad. Nat. Sci. Philadelphia 76: 53, text-fig. 1d. Found only in Lake Titicaca, Peru (HAAS, 1955).

Strombopoma titicacae "HAAS," HUBENDICK, 1955. Trans. Linn. Soc. London, ser. 3, 1: 323, 325, text-figs. 81-82, 90. Nomen nudum. = *S. ortonii* (PILSBRY).

Texadina ABBOTT & LADD, 1951

Jour. Wash. Acad. Sci. 41: 335. Type (O.D.): *Littoridina sphinctostoma* ABBOTT & LADD.

The peristome is constricted, and the last third of the body whorl descends more rapidly than in typical *Littoridina*. Other than the radula, operculum, and general shape of the head, the anatomy is unknown. *Texadina* may perhaps prove to be a senior synonym of *Littoridinops* when other details of its anatomy are known.

Texadina sphinctostoma (ABBOTT & LADD), 1951 (*Littoridina*). Jour. Wash. Acad. Sci. 41: 335, text-figs. 1-12. Brackish waters in the vicinity of Rockport and Aransas Pass, Texas, and Grand Isle, Louisiana, U.S.A. Subsequently reported from other Louisiana localities by SOLEM (1961) and KEITH & PARKER (1965).

Tryonia STIMPSON, 1865

Tryonia STIMPSON, 1865. Amer. Jour. Conch. 1: 54. Type (O.D.): *T. clathrata* STIMPSON.

Isaea CONRAD, 1871. Amer. Jour. Conch. 6: 193. Type (here designated): *Mesalia ortonii* GABB, 1869. Not of EDWARDS, 1830.

Liris CONRAD, 1871. Amer. Jour. Conch. 6: 193. Type (M.): *Liris laqueata* CONRAD.

Dyris CONRAD, 1871. Amer. Jour. Conch. 6: 195. Type (M.): *Dyris gracilis* CONRAD.

Conradia WENZ, 1925. Senckenbergiana 7: 125. New name for *Isaea* CONRAD, not EDWARDS. Not of A. ADAMS, 1860.

Shell turritiform, with more whorls, a narrower outline, smaller aperture, and deeper suture than in most *Pyrgophorus*. The sculpture may consist only of growth line, or may be coarsely lirate, plicate, or reticulate. Spines on the shoulder of the shell (characteristic of *Pyrgophorus*) are unknown in *Tryonia*.

Virtually all of the species are known by shell alone, so that no trenchant characterization of the genus is possible. *Tryonia cheatumi* is known to be ovoviviparous like *Pyrgophorus* (PILSBRY, 1935b).

Most of the range of *Tryonia* is within the high plateaus of southwestern North and Central America that now have internal drainage (Great Basin in western U.S.A.; Laguna Petén-Itza, Dept. Petén, Guatemala) or that drain to the Pacific Ocean. The only occurrences in Atlantic drainage are those in the Pecos River valley (tributary to Rio Grande), New Mexico and Texas, U.S.A.; a Tertiary occurrence on Río Carboneras, tributary to Lake Izabal, Guatemala, and so to the Caribbean (DALL, 1924a, b); and the South American records. Nearly all of these localities are in regions where there are, or were in late Tertiary times, extensive lake basins.

Tryonia amazonica (HAAS, 1949) (*Potamopyrgus*). An. Inst. Biol. Mex. 20: 313; text-fig. 6. Río Tapajóz, Balterra, Pará, Brasil.

Tryonia bakeri (PILSBRY, 1891) (*Potamopyrgus*?). Nautilus 5: 9. Proc. Acad. Nat. Sci. Philadelphia 43: 328, pl. 15, figs. 9-11. Subfossil, streambank east of Yautepec, Morelos, México.

Tryonia bicarinata (ETHERIDGE, 1879) (*Melania*). Quart. Jour. Geol. Soc. London 35: 88, pl. 7, fig. 7. Pliocene?, Canama, Prov. Loreto, Perú. Referred by WENZ (1926) to *T. tricarinata*, but DE GREVE (1938) doubted such an assignment.

Pyrgulopsis blakeana TAYLOR, 1950. Leaf. Malac. 1: 30, text-figs. 4-6. Subfossil, Fish Springs, Imperial County, California, U.S.A. = *Tryonia protea* (GOULD).

Pyrgulopsis cahuillarum TAYLOR, 1950. Leaf. Malac. 1: 31, text-fig. 7. Subfossil, 7.9 miles west of Mecca, Colorado Desert, California, U.S.A. = *Tryonia protea* (GOULD).

Tryonia cheatumi (PILSBRY, 1935) (*Potamopyrgus*). Nautilus 48: 91, text-fig. 4. Phantom Lake, near Toyahvale, Reeves County, Texas, U.S.A.

Tryonia circumstriata (LEONARD & Ho, 1960b) (*Calipyrgula*). Nautilus 73: 125, pl. 12, figs. 1-3. Late Pleistocene terrace deposits along Pecos River 1/4 mile above

mouth of Independence Creek, on Chandler Ranch, Terrell County, Texas. Also known from 2 other localities as a fossil in Terrell and Pecos Counties, Texas, U.S.A.

Tryonia clathrata STIMPSON, 1865. Amer. Jour. Conch. 1: 54; pl. 8, fig. 1. The type locality was given as the Colorado Desert, California. In the light of present knowledge most likely the original subfossil material came from near the lower course of the Muddy River, Clark County, Nevada, U.S.A. The species lives only in the Pahrnagat Valley, southern Nevada.

Tryonia confusa (BOETTGER, 1878) (*Hydrobia*). Jahrb. k.-k. geol. Reichsanst. 28: 491, pl. 13, figs. 4a, b, 6a, b, 7a-c. Pliocene?, Pebas, Prov. Loreto, Perú. Reported also from Iquitos, Prov. Loreto, by DE GREVE (1938).

Paludestrina curta ARNOLD, 1903. Mem. Calif. Acad. Sci. 3: 305, pl. 8, fig. 2. Pleistocene, San Pedro Sand and Palos Verdes Sand, San Pedro, Los Angeles Co., California. = *Tryonia imitator* (PILSBRY) according to TAYLOR (1966a).

Tryonia exigua (MORELET, 1851) (*Melania*). Testacea novissima 2: 23. Laguna Petén-Itza, Dept. Petén, Guatemala.

Melania exigua CONRAD, 1855. Proc. Acad. Nat. Sci. Philadelphia 7: 269. Colorado Desert, California, U.S.A. (subfossil). = *Tryonia protea* (GOULD). Preoccupied by *Melania exigua* MORELET, 1851, also a *Tryonia*.

Tryonia jagundesii (HAAS, 1938) (*Potamopyrgus*). Arch. Molluskenk. 70: 50, text-figs. 8-9. Recife, Pernambuco, Brasil. Recorded from the same area by HAAS (1939).

Tryonia gracilis (CONRAD, 1871) (*Dyrus*). Amer. Jour. Conch. 6: 195, pl. 10, fig. 8; pl. 11, fig. 7. Pliocene? Pichua, below Pebas, Prov. Loreto, Peru. Reported also from Canama, Pebas, and Iquitos, all Prov. Loreto, Peru (BOETTGER, 1878; ETHERIDGE, 1879; DE GREVE, 1938).

Tryonia imitator (PILSBRY, 1899) (*Paludestrina*). Nautilus 12: 124. Santa Cruz, Santa Cruz Co., California. Published and unpublished records indicate a range from San Francisco Bay to San Diego County, California, in brackish water, and a geologic range as far back as the late Miocene or early Pliocene (OAKESHOTT, 1958).

Alabina io BARTSCH, 1911. Proc. U.S. Nat. Mus. 39: 415, pl. 61, fig. 1. Originally stated to be from Pleistocene deposits at San Diego, San Diego County, California, but according to WOODRING *et al.* (1946:67) it is from San Pedro, Los Angeles County, California, U.S.A. The stratigraphic horizon of the type is unknown; it might be upper or lower Pleistocene. = *Tryonia stokesi* (ARNOLD) according to TAYLOR (1966a).

Tryonia lacirana (PILSBRY & OLSSON, 1935) (*Potamopyrgus*). Proc. Acad. Nat. Sci. Philadelphia 87: 9, pl. 5,

fig. 6. Upper Oligocene or lower Miocene, La Cira Formation, La Cira district, Prov. Santander, Colombia.

Tryonia laqueata (CONRAD, 1871) (*Liris*). Amer. Jour. Conch. 6: 194, pl. 10, fig. 3. Pliocene?, Pichua, below Pebas, Prov. Loreto, Peru. Reported also from Iquitos, Prov. Loreto, Peru (DE GREVE, 1938).

Tryonia lineata (CONRAD, 1871) (*Isaca*). Amer. Jour. Conch. 6: 193, pl. 10, fig. 6. Pliocene? Pichua, below Pebas, Prov. Loreto, Peru. Reported also from Iquitos, Prov. Loreto, Peru (DE GREVE, 1938).

Tryonia minuscula (GABB, 1869) (*Turbonilla*). Amer. Jour. Conch. 4: 197, pl. 16, fig. 1. Pliocene?, Pebas, Prov. Loreto, Peru. Reported also from Canama, Tres Unidos, and Iquitos, Prov. Loreto, Peru; and Rio Quixito and Cachocha das Fracoas, Amazonas, Brasil (ETHERIDGE, 1879; ROXO, 1924; DE GREVE, 1938).

Melania minuta BROU, 1862. Matériaux . . . Catalogue systématique . . . des Mélaniens: 43. New name for *Melania exigua* (MORELET) as described by REEVE (1861). = *Tryonia exigua* (MORELET) according to FISCHER & CROSSE (1870-1902).

Tryonia ortonii (GABB, 1869) (*Mesalia*). Amer. Jour. Conch. 4: 198, pl. 16, fig. 3. Pliocene?, Pebas, Prov. Loreto, Perú. Reported also from Pichua and Iquitos, Prov. Loreto, Peru (CONRAD, 1871; DE GREVE, 1938).

Tryonia patzcuarensis (PILSBRY, 1891) (*Pyrgulopsis?*). Nautilus 5: 9. Proc. Acad. Nat. Sci. Philadelphia 43: 330, pl. 15, fig. 8. Lake Patzcuaro, Michoacán, México.

Tryonia pecosensis (LEONARD & HO, 1960a) (*Calipyr-gula*). Nautilus 73: 110, pl. 11, fig. 1-3. Late Pleistocene terrace deposits along Pecos River, 3.5 miles northeast of Imperial, Crane County, Texas. Also known from 5 other localities as a fossil in Pecos and Ward Counties, Texas, U.S.A.

Tryonia protea (GOULD, 1855) (*Amnicola*). Proc. Boston Soc. Nat. Hist. 5: 129. Subfossil, Colorado Desert, California, U.S.A.

Tryonia scalarioides (ETHERIDGE, 1879) (*Melania*). Quart. Jour. Geol. Soc. London 35: 88, pl. 7, fig. 8. Pliocene? Canama, Prov. Loreto, Peru.

Tryonia stokesi (ARNOLD, 1903). Mem. Calif. Acad. Sci. 3: 22, 23, 44, 305, pl. 8, fig. 3 (*Paludestrina*). Lower Pleistocene, San Pedro Sand, San Pedro, Los Angeles County, California, U.S.A.

Tryonia tricarinata (BOETTGER, 1871) (*Hydrobia*). Jahrb. k.-k. geol. Reichsanst. 28: 492, pl. 13, figs. 10a, b, 11a-c. Pliocene?, Pebas, Prov. Loreto, Peru. Reported also from Canama and Iquitos, Prov. Loreto, Perú (ETHERIDGE, 1879; DE GREVE, 1938).

Tryonia tuberculata (DE GREVE, 1938) (*Liris*). Abh. Schweiz. Paleont. Gesellsch. 61 (3): 96, 125, pl. 2, figs.

32-35; pl. 3, figs. 1-20; text-fig. 19-22. Pliocene? Iquitos, Prov. Lorcto, Peru.

Zetekina MORRISON, 1947

Zetekella MORRISON, 1946. *Smithson. Misc. Coll.* 106 (6): 11. Type (O.D.): *Zetekella frenata* (PILSBRY). Not of DRAKE, 1944.

Zetekina MORRISON, 1947. *Nautilus* 60: 102. New name for *Zetekella* MORRISON, 1946, not DRAKE, 1944.

The verges of *Zetekina frenata*, *Z. kompi*, and *Z. veraguasensis* have been figured by MORRISON (1946) and PILSBRY (1935b). The modern distribution of the genus is in the Pacific drainage from Nicaragua to central Panamá and the Pearl Islands, Panamá; a Pliocene species is known from California, U.S.A.

Zetekina frenata (PILSBRY, 1935) (*Littoridina*). *Proc. Acad. Nat. Sci. Philadelphia* 87: 5, text-figs. 1, 1a. Río Juan Diaz, Panamá.

Zetekina kompi (MORRISON, 1946) (*Zetekella*). *Smithson. Misc. Coll.* 106 (6): 13, pl. 2, fig. 2; pl. 3, fig. 2. Río Mata Puerco, San José Island, Archipiélago de las Perlas, Panamá.

Zetekina martensi (PILSBRY, 1935) (*Littoridina*). *Proc. Acad. Nat. Sci. Philadelphia* 87: 5, text-fig. 2. Río Fula, Nicaragua. So assigned by MORRISON (1946).

Zetekina melanioides (MARTENS, 1899) (*Amnicola?*). *Biol. Centr.-Am., Moll.*: 436, pl. 22, fig. 8. Río de los Platanales, Golfo Dulce, Costa Rica. So assigned by MORRISON (1946).

Zetekina panamensis (BARTSCH, 1920) (*Syncera*). *Proc. U.S. Nat. Mus.* 58: 164, pl. 12, fig. 8. Río Matasnillo, Panamá. So assigned by MORRISON (1946).

Zetekina tenuis (MARTENS, 1899) (*Amnicola?*). *Biol. Centr.-Amer., Moll.*: 436, pl. 22, fig. 9. Tributary of Río Boto at Golfo Dulce, and marshes of Seripe, Costa Rica. Considered of specific rank by PILSBRY (1935).

Zetekina veraguasensis (MORRISON, 1946) (*Zetekella*). *Smithson. Misc. Coll.* 106 (6): 12, pl. 2, fig. 1; pl. 3, fig. 1. Río Tribique, Sona, Veraguas Prov., Panamá.

Zetekina woodringi (PILSBRY, 1934) (*Littoridina*). *Nautilus* 48: 16. PILSBRY, 1935, *Proc. Acad. Nat. Sci. Philadelphia* 86: 558, pl. 21, fig. 3, 4. Late Pliocene, basal part of Tulare Formation, Kettleman Hills, California, U.S.A. So assigned by TAYLOR (1966a).

The verge is known only by the description and illustrations published by MORRISON (1946) and PILSBRY (1935c). So far as one can interpret them, there is a very short, melanin-pigmented free part of the penis, as in *Mexipyr-gus* and at least some *Tryonia*; and 2 bulbous or elongate accessory processes on the left side near the distal end,

as in *Durangonella*. From these meager data, and from geographic distribution, the genus appears most likely to be one of the Littoridininae. The radula is still unknown.

Littoridininae?, incertae sedis

One broken and bleached shell (UMMZ 220178) was found in a bottom sample from the northernmost pool of Pozos de la Becerra, 18 km southwest of Cuatro Ciénegas, Coahuila, México, collected by C. L. Hubbs, 6-IV-1961. The specimen measures 0.6 x 0.5 mm, with 2½ whorls that are nearly circular in cross-section, separated by a deeply incised suture, and retain ornament of growth lines only. The shell is far too narrow and has more whorls for its size than *Mexipyr-gus*. The nearest form is *Durango-nella*, but the species of that genus in the Cuatro Ciénegas valley have whorls that lengthen more rapidly and are more oval in cross-section. This single shell evidently represents a species otherwise unknown in the area, perhaps *Durangonella* or some other genus.

Lyogyrinae

Shell trochoid to turritiform, with whorls nearly circular in cross-section, separated by a deeply incised suture; operculum multispiral as in *Valvata*, more tightly coiled than in Cochliopinae.

Referred genera: The one genus included is *Lyogyrus* GILL, 1863, known from the Atlantic and Gulf coasts of the U.S.A., from Massachusetts to Alabama.

WALKER (1918) attributed the name Lyogyrinae to PILSBRY (1916); this reference is a bare mention of the name, and WALKER seems to be the taxonomic author of the group.

Lyogyrus GILL, 1863

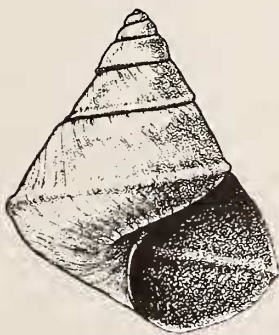
Proc. Acad. Nat. Sci. Philadelphia 15: 34. Type (O.D.) *Valvata pupoidea* GOULD. Described as genus of Valvatidae.

Literature on the 5 nominal species is accessible through WALKER (1918) and VANATTA (1934).

Virtually nothing is known of this group. The radula has been briefly mentioned by PILSBRY (1888, 1892) as like that of the Hydrobiidae instead of the Valvatidae, and for this reason the genus has been so classified ever since. If GOULD (1841: 227) correctly described the ctenidium as protrusible, then *Lyogyrus* cannot be one of the Hydrobiidae and might indeed show characters in common with Valvatidae. But from the fact that Gould stated the respiratory organ was protruded on the right, I suspect his observation is based on misidentification of the verge, or perhaps a pallial tentacle on the right side.

Nymphophilinae TAYLOR, new subfamily

Shell large for the family, attaining a length of 10 mm, trochoid, narrowly phaneromphalous, with a flat-sided spire and a single persistent spiral carina. Operculum (Text figure 20) multispiral with a central nucleus. Vas deferens in a raised ridge on the floor of the mantle cavity, rather than beneath it. Verge (Text figure 21) with glandular accessory process, and a free part of the penis that is relatively mobile and distensible for the family and contains a noticeable blood sinus. Eggs single in smooth, hemispherical capsules.



Figures 17 to 19

Nymphophilus minckleyi TAYLOR, gen. et spec. nov.

Type, UMMZ 220183. Length 7.0 mm; width 6.0 mm; $5\frac{3}{4}$ whorls.

Referred genera. *Nymphophilus* TAYLOR, gen. nov., is the only included genus. The subfamily is thus known only from the valley of Cuatro Ciénegas, Coahuila, México.

Establishing a new subfamily for this unusual genus would not be warranted on shell characters alone, but there are some features unique in the family, and others that are rare. The multispiral operculum is a distinctive character, otherwise known in American Hydrobiidae only in the Cochliopinae and Lyogyrinae. The shell is remarkably large for the family, equaled only in Lithoglyphinae, and most un-hydrobiid in general appearance; it reminds one more of the marine Trochidae. The shape of the verge is not distinctive—it might belong to the Hydrobiinae—but the distensible penis and evident blood sinus are not like any Hydrobiidae I have studied or found in the literature. The course of the vas deferens in a ridge on top of the mantle cavity floor is unique, and seemingly not correlated with other structures.

***Nymphophilus* TAYLOR, gen. nov.**

Diagnosis. Same as for the subfamily.

Type. *Nymphophilus minckleyi* TAYLOR, spec. nov. No other species are known in the genus.

Etymology. The name is from *Nymphaea*, the water-lily; and Greek *philos*, beloved, dear. The genus is characteristically found on *Nymphaea* leaves in the lagunas of the Cuatro Ciénegas region.

***Nymphophilus minckleyi* TAYLOR, spec. nov.**

(Plate 13, Figures 15, 17; Text figures 17-21)

Diagnosis. Same as for the subfamily.

Type. UMMZ 220188. Coahuila, México: Río Mesquites at the main road 9 km southwest of Cuatro Ciénegas. D. W. Taylor, 13-IV-1965. The same collection yielded a number of other specimens, some of which were destroyed for cytological or morphological study; those preserved are UMMZ 220189. The locality is number 11 on Text figure 2.

Localities and material examined (listed in geographic sequence around Sierra de San Marcos, beginning at the southwest).

Laguna Churince, 16 km SW Cuatro Ciénegas; D. W. Taylor, 12-IV-1965 (UMMZ 220154).

Unnamed laguna west of Río Churince; D. W. Taylor, 14-IV-1965 (UMMZ 220156).

Pozos de la Becerra, 14 km SW Cuatro Ciénegas; C. L. Hubbs, 6-IV-1961 (UMMZ 220175); W. L. Minckley,

28-XII-1964 (UMMZ 220172); D. W. Taylor, 14-IV-1965 (UMMZ 220169).

⁸Río Mesquites, 9 km SW Cuatro Ciénegas; D. W. Taylor, 13-IV-1965 (UMMZ 220188, 220189).

West Laguna in El Mojarral, 1.7 km ENE of tip of Sierra de San Marcos; D. W. Taylor, 13-IV-1965 (UMMZ 220196).

East Laguna in El Mojarral, 1.9 km ENE of tip of Sierra de San Marcos; D. W. Taylor, 13-IV-1965 (UMMZ 220201).

⁹Laguna Escobeda, 12 km S of Cuatro Ciénegas; W. L. Minckley, 31-XII-1964 (UMMZ 220210); D. W. Taylor, 15-IV-1965 (UMMZ 220207).

⁹Laguna Tío Candido, 14 km S Cuatro Ciénegas; D. W. Taylor, 15-IV-1965 (UMMZ 220216).

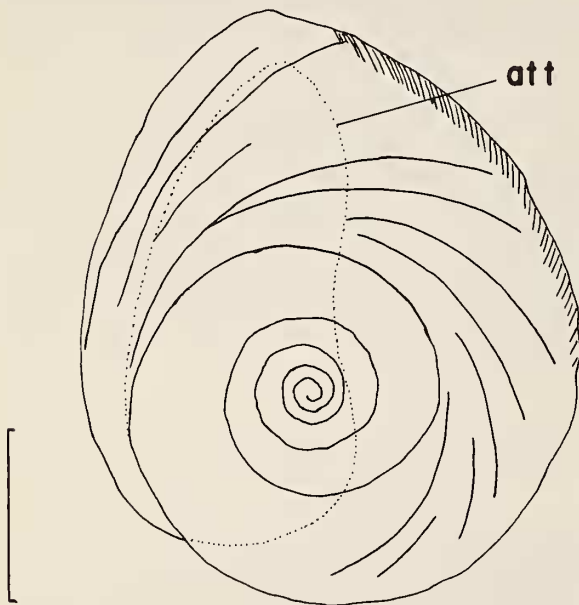


Figure 20

Operculum of *Nymphophilus minckleyi* TAYLOR, gen. et spec. nov., external view;

scale line = 1.0 mm. att - border of attachment to foot.

General form, locomotion, behavior. The conical shell about 10 mm long in adults is borne free of the substratum with the apex directed upward and posteriorly to the right, so that the axis of the shell forms an angle of about

45-60 degrees with the long axis of the foot. In dorsal view when the snails are crawling the tip of the snout, most of the length of the tentacles, and the hind end and anterior corners of the foot are visible. The eyes are not usually visible in this view. Compared to other Hydrobiidae seen the snails crawl at moderate speed; they move smoothly and do not show the stepwise gait of the Pomatiopsinae. The animal can right itself only with difficulty when turned on its back.

The tentacles are nearly as long as the aperture, and taper gently to rounded tips. They show no definite arrangement of cilia. The tentacles are borne diverging at an angle of about 90-120 degrees, and usually are in vertical or horizontal movement. They move both above and below a plane parallel to the substratum, and often touch the substratum as if sensing it. In crawling the snail keeps its snout appressed to the substratum, and moves it from side to side while browsing. The movement of the radula can be seen within the translucent snout.

Pigmentation. The shell and external body are a similar light ochre color in gross aspect. The shell is translucent, so that some internal structures can be seen through the shell, but the organs contain so little pigment that none of them can be discerned clearly. Elements of color are very fine granules of melanin, mostly occurring as a thin dust in the surface epithelium of the head-foot mass, and larger hyaline granules that are scattered in the tissue and appear pale yellow.

The sole of the foot appears very pale yellow-gray. The central part is clear and translucent, but the sides and hind part contain scattered yellowish hyaline granules and melanin granules that give it a darker hue. The anterior edge is clear like the central area, so that the mucus glands can be seen within the foot. In ventral view the operculigerous lobe appears darker than the borders of the sole, from more abundant melanin and hyaline granules.

The sides and top of the head-foot area are lightly coated with brown-appearing melanin granules. Together with the abundant hyaline granules in the tissue they give the body its ochre color. No definite pattern is evident, except that the melanin and hyaline granules are a little more heavily concentrated behind the eyes.

Head-foot mass. The foot is about twice as long as wide, with a constriction behind the anterior corners and a broadly rounded posterior end. The anterior mucous glands are visible through the sole, emptying into the anterior pedal groove. The snout is short and tapers conspicuously. Its width at the base of the tentacles is about equal to its length from the mouth to the tentacles. The outline of the reddish-brown buccal mass can be seen within, and the esophagus extending posteriorly. In cross-section the snout is oval, more convex dorsally. The fleshy pad at the

⁸ Population studied from living specimens as well as relaxed, fixed material.

⁹ Population extinct.

anterior end is separated from the rest of the snout by a narrow incised groove, and divided in two by the slit of the mouth.

The tentacles are stout and taper regularly to rounded tips. They are circular in cross-section toward the tips, but oval and flattened dorso-ventrally toward the base. Cilia are uniformly distributed on their surface. The eyes lie in prominent discrete swellings on the outer bases of the tentacles.

The operculigerous lobe is indistinct, not separated from the rest of the foot by grooves or special ciliated areas. In ventral view the lobe appears as a couple of buttress-like swellings that run from the dorsal edge of the sole to the anterior-lateral regions of the operculum. The operculum overhangs the operculigerous lobe from the farthest lateral projections of the lobe on around behind.

Mantle cavity. The edge of the mantle is thickened to form a collar, but is otherwise smooth. The collar contains abundant hyaline granules and is suffused with fine melanin granules. An observer looking into the cavity of a living snail can see the ctenidium, anus and distal part of the rectum, and verge; the osphradium and end of the female genital system are visible only on close inspection. No grooves lead in or out of the mantle cavity, but a ciliated tract runs out of the mantle cavity down the right side of the head-foot to the edge of the sole. As usual, circulation of water is in on the left and out on the right.

The ctenidium extends farther toward the edge of the mantle cavity than any other structure in it, except for the verge when that is extended. The most distal lamellae in the ctenidium are attached to the mantle next to the collar. The ctenidium as a whole consists of about 40 lamellae, each in the form of an acute triangle hanging from the mantle and pointing toward the floor of the cavity. The ctenidium runs the length of the cavity, dividing it into 2 equal parts; the right margin of the ctenidium lies below the peripheral carina on the shell.

The anus lies about $\frac{1}{8}$ whorl within the aperture. The rectum is attached to the mantle throughout its course, and lies in the angle of the mantle cavity next to the suture.

Male reproductive system. The male reproductive system in *Nymphophilus* consists of the organs common to Hydrobiidae in general. The testis in the upper visceral mass produces sperms which are led through a collecting duct into that part of the upper vas deferens specialized as a seminal vesicle, thence through the upper vas to the prostate, then through the lower vas on the floor of the mantle cavity into the verge. The special features of the animal are the course and size of the lower vas deferens, and the details of shape and structure of the verge.

The testis lies in the posterior $\frac{1}{2}$ to $\frac{2}{3}$ of the first and second whorls. It is closely appressed to the very pale gray digestive gland from which it is readily distinguished by its bright yellow color. The testis does not extend to the tip of the visceral mass; the first half whorl and the anterior parts of the next $1\frac{1}{2}$ whorls are taken up by the digestive gland.

The digitiform follicles making up the testis discharge via the vasa efferentia into a common collecting duct. The duct leaves the columellar aspect of the testis at about midlength. This structure contrasts with that in some other Hydrobiidae, in which the follicles discharge in several groups into a duct leaving the testis at its proximal end.

The pale, narrow, thin-walled common collecting duct enlarges rapidly after its emergence from the testis into a thick-walled, highly convoluted tube 2-3 times its previous diameter. This tube is the part of the upper vas deferens specialized as a seminal vesicle. The lumen is about $\frac{3}{4}$ the diameter of the tube, and crowded with sperm readily visible as a white mass through the translucent walls of the vesicle. The seminal vesicle lies in the columellar aspect of the visceral mass for about one whorl, extending to the level of the stomach.

The upper vas deferens narrows gradually, and the white mass of sperm inside becomes progressively narrower, until it is again a pale, narrow, thin-walled tube like the collecting duct. Here it leaves the visceral mass proper, and enters a dense mass of connective tissue dorsal to the hind end of the columellar muscle, ventral to the prostate gland, just behind the visceral ganglion and to the right of the hind end of the mantle cavity. It enters the prostate gland at about mid-length on the ventral side.

The prostate gland is a whitish elongate-body of loose texture that lies next to the right hind end of the mantle cavity, but does not project into it. The visceral ganglion lies directly beneath it.

The lower vas deferens emerges from the prostate on the ventral side at nearly midlength, close in front of the entrance of the upper vas into the prostate. The lower vas then runs in the right wall of the mantle cavity, first anteriorly, then ventrally, to the floor of the mantle cavity at about mid-length of that cavity. The lower vas is a tube obviously thicker than the upper vas where it enters the prostate, but only about half as thick as the seminal vesicle, and with less translucent walls. On reaching the floor of the mantle cavity the vas deferens runs as a raised ridge on the floor of the mantle cavity, first to the left until it reaches a sagittal plane through the base of the right tentacle, and then anteriorly nearly to the front of the mantle cavity. Here it bends posteriorly and to the left, and enters the right edge of the

verge. The raised ridge on the floor of the mantle cavity is nearly semicircular in cross-section, slightly sinuous in its course, and but slightly larger in diameter than the vas deferens. Seemingly the vas is simply applied to the floor of the mantle cavity, rather than lying beneath it as is the case in all other known Hydrobiidae. An observer can look into the mantle cavity of a living snail that is suitably extended out of the shell, and see even at low magnification the shimmering light refracted from cilia beating in the vas deferens before it enters the verge.

The verge (Text figure 21) is a large organ nearly filling the mantle cavity. It consists of a dorso-ventrally flattened, transversely wrinkled base; a small, glandular accessory process on the left; and a tubular structure as long as or longer than the base that is the free part of the penis.

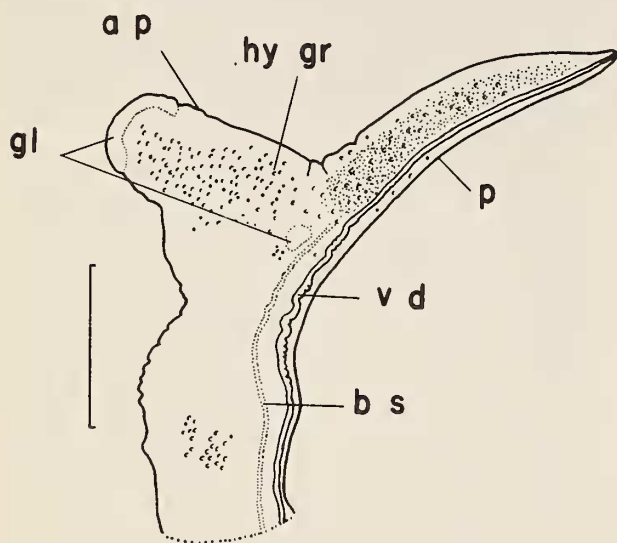


Figure 21

Verge of *Nymphophilus minckleyi* TAYLOR, gen. et spec. nov., dorsal view. Scale line = 1 mm. a p - accessory process; b s - blood sinus; gl - glandular area; hy gr - hyaline granule; p - free part of penis; v d - vas deferens.

The base of the verge is inserted transversely on the floor of the mantle cavity, with the left edge slightly to the left of the median plane. The right edge is in a sagittal plane through the left side of the base of the right tentacle, and slightly posterior to the left edge of the verge. The width of the verge base is about 5 times its antero-posterior thickness.

The verge is normally carried pointing normal to its attachment. Thus, owing to the oblique insertion, the accessory process points forward between the tentacles while the free part of the penis points to the right of the right tentacle. As observed in living specimens, the penis is more mobile and distensible than in any other Hydrobiidae studied. In correlation with the ability to lengthen and move is the occurrence of a discrete blood vessel running to the left of the vas deferens through the base of the verge into the free penis. Such a vessel, appearing as a second tube in the verge, is unknown in other Hydrobiidae.

The base of the verge is unpigmented, very pale gray, and transversely wrinkled. Large yellowish hyaline granules may be clumped near the insertion. The smaller, translucent granules in the accessory process and free penis are not evident in the base.

The short accessory process is unpigmented but contains scattered translucent hyaline granules. The distal end is made up of glandular tissue, appearing milky and nearly opaque. The glandular area may consist of a single band along all of the distal end of the accessory process, or it may be separated into 2 or 3 discrete areas. In one instance a small glandular area occurred also at the base of the accessory process. The process is flattened dorso-ventrally, and is about as thick as the base of the verge, or about 4 times as wide as thick.

The free part of the penis is superficially coated with a dust of fine melanin granules that give it a light ochre color, similar to that of the external parts of the body. It contains numerous scattered translucent hyaline granules like those in the accessory process. The free penis is circular in cross-section, with the vas deferens close to its right side and opening at the tip through a simple pore.

Eggs. Only 2 egg capsules were found, both on the shells of living *Nymphophilus*. *Nymphaea* leaves collected in the hope of finding eggs yielded none. The capsules were hemispherical, smooth with no evident surface texture, and appressed to the shell surface with no evident special attachment area. Each was about 0.55 mm in diameter, 0.4 mm high, and contained a single embryonic snail.

Habitat. *Nymphophilus* was found alive at 7 localities. At all but one of these the water-lily *Nymphaea* was present, and *Nymphophilus* was most common or found only on the under sides of the lily pads characteristically at a depth of 0.5 m or more. In the laguna west of Rio Churince (Text figure 2, locality 9) no water lilies were seen. Here *Nymphophilus* was found only on the lower surfaces of limey algae masses and tufa, in a habitat like that where some specimens were found in West Laguna in El Mojarral (Text figure 2, locality 5).

Food and feeding. The *Nymphaea* leaves on which *Nymphophilus* was common were seen in the field to have holes of irregular shape and up to about 10 mm long. Both leaves and snails were brought to the laboratory, but the snails did not survive the trip long and no definite observations could be made. In the laboratory the snails did eat fresh lettuce, from which it seems possible that they do eat lily pads rather than merely browse on the epiphyton.

Etymology. The species is named in honor of W. L. Minckley, Arizona State University, Tempe, Arizona, U. S. A.

Pomatiopsinae¹⁰ STIMPSON, 1865

Verge with only 1 duct, the vas deferens (contrast Amnicolinae and Fontigentinae), without accessory processes. Eyes in relatively prominent bulbous swellings on the outer bases of the tentacles, set off anteriorly by a slight crease (contrast all other subfamilies). Pigmentation consists only of melanin; no yellow granules are present in the head-foot (contrast (Lithoglyphinae). Operculum corneous, paucispiral (contrast Cochliopinae, Lyogyrinae, Nymphophilinae). Shell turritiform, phaneromphalous; aperture simple or with a varix. Eggs are laid singly in smooth capsules coated with a husk of mud. The sides of the head-foot are subdivided by 2 prominent grooves: a longitudinal groove begins at the base of the rostrum and runs posteriorly beneath the operculigerous lobe; the other, oviducal groove extends ventrally along the sides of the body stalk as in other subfamilies, but terminates abruptly at the longitudinal fold. Progression is step-wise, in correlation with an amphibious or terrestrial habitat (contrast other subfamilies). Central tooth of radula with 2-3 basal cusps borne on antero-posterior ridges, not on a lateral angle (contrast all other subfamilies). Cusps of lateral and marginal teeth few in number for Hydrobiidae (3-11 marginal cusps).

The scope of the Potamiopsinae has been increased since STIMPSON (1865) defined the group, but his original diagnosis is substantially valid. GILL (1871) and a few later authors (for example F. C. BAKER, 1928; E. G. BERRY, 1943) have ranked Pomatiopsinae as a family, but I concur with DAVIS (1965) that subfamily rank is more appropriate.

Three characters of the Pomatiopsinae are especially distinctive: the longitudinal groove along the sides of the body, the position of the basal cusps of the central tooth, and the prominent eye-swellings. Additional morpholog-

ical data on many Rissoacean groups will be necessary to assess these characters, but some suggestions to stimulate further research are worthwhile.

The longitudinal groove along the sides of the body is unknown in other Hydrobiidae, but reminiscent of a similar groove in the Assimineidae. Unless this groove can be ascribed plausibly to parallel adaptation to the semiaquatic environment in which both groups generally live, the probability of common inheritance of this character should be considered.

The basal cusps of the central tooth have a location and morphologic origin different from that in all other Hydrobiidae, and hence they are probably not homologous. Perhaps then the radula of Pomatiopsinae has been derived from one lacking basal cusps, i. e., from a family other than Hydrobiidae as defined herein. In considering the radula of Pomatiopsinae, one should recall that the radula of Bithyniidae (a family profoundly different from Hydrobiidae in many characters) is more like that of most Hydrobiidae than is the radula of Pomatiopsinae.

The prominent swellings in which the eyes are borne are unlike those of other American Hydrobiidae. STIMPSON (1865) described *Potamopyrgus* as having the eyes in prominent tubercles, but no comparison of that genus with Pomatiopsinae nor detailed description has been published.

Referred genera (references are available in WENZ, 1938 to 1944, or in the bibliography of this paper):

Blanfordia A. ADAMS, 1863. Japan.

Oncomelania GREDLER, 1881 (including *Schistosomophora* BARTSCH, 1936). Eastern Asia.

Pomatiopsis TRYON, 1862. U. S. A.

Tomichia BENSON, 1851. South Africa.

Unnamed subfamily?

Shell turritiform, with an expanded outer lip.

Referred American genera: *Emmericiella* PILSBRY, 1909. San Luis Potosí, México (2 species).

Pterides PILSBRY, 1909. San Luis Potosí, México (3 species).

A number of European genera, particularly in the Balkans, share the unusual character of an elongate, turritiform to aciculate shell with a flaring aperture. These may form a group that can be usefully named, but until more is known of their anatomy formal establishment of the group would be unwise. PILSBRY (1909) interpreted *Pterides* as a relative of such forms as *Lartetia*, with which I agree; but he referred *Emmericiella* to *Emmericia* as a subgenus, thus to the Emmericiinae in Micromelaniidae. Judging entirely from illustrations *Emmericiella* is more similar to such Hydrobiidae as *Plagigeyeria* and *Microsal-*

¹⁰ The differentia and scope of this group have been mainly accepted from the work by DAVIS (1965).

pinx than to *Emmericia*; and I hesitate to recognize Micro-melaniidae in North America on such slender grounds as *Emmericiella* alone.

Lartetia was cited by MORRISON (1949) as occurring in eastern North America, but no descriptions or illustrations of the species have been published.

HYDROBIIIDAE?

Mexithaumatinae TAYLOR, new subfamily

Diagnosis. Shell globose, helicoid, up to about 7.5 mm long with $4\frac{1}{2}$ whorls, anomphalous. Sculpture consists of about 10-12 spiral cords spaced at nearly equal distance; with increase in size of the shell the number of cords increases by intercalation. The periostracum is brown between cords. On each cord the periostracum is produced into a very dark brown, nearly black, spiral ridge bearing a linear series of short bristles. Operculum plane, corneous, paucispiral. Mantle edge with low papillae, each corresponding to a cord on the shell. Eyes in outer bases of the tentacles, closer to the base and in a less conspicuous swelling than usual in Hydrobiidae. No concentration of hyaline granules around the eye, as is usual in Hydrobiidae. Tentacles with a dorsal lengthwise stripe of melanin, from just beyond the eye nearly to the tip. The verge (Text figure 22) is simple, with no accessory glands or

ducts; it has a narrow distal moiety in which the vas deferens is narrower than in the broader base. The pallial oviduct runs parallel to the rectum, then turns ventrally and posteriorly to the floor of the mantle cavity. The snails are ovoviviparous.

Referred genera. *Mexithauma* TAYLOR, gen. nov., is the only included genus.

Discussion. There are a number of unique and unusual features of this snail. Evidently it is not much like any known Hydrobiidae, and for convenience in defining that family, *Mexithauma* ought to be excluded. Yet there are no clear evidences of relationship to any other neighboring Rissoacean family, so for the present this snail is left in the Hydrobiidae by default.

Three important characters of *Mexithauma* are otherwise unknown in the Hydrobiidae. These are the papillose mantle border, the reflected end of the pallial oviduct, and the bristly periostracum. I am not certain that analogous characters outside the Rissoacea are of great significance, but it is worth noting that one of the long-time distinctions between Pleuroceridae and Thiariidae (Cerithiacea) is that the former has a plain, the latter a papillose mantle border. The lower course of the oviduct is anomalous; a similar condition is unknown in the other Rissoacea. The surface texture of the periostracum seems to be a weighty character. In only 1 genus described in the Hydrobiidae is the periostracum not smooth-textured: *Antroselates* HUBRICHT (1963). This genus has a central tooth of the radula without basal denticles, and hence I

Explanation of Plate 18

Mexipyrus from the Valley of Cuatro Ciénegas, Coahuila.

Photographed by K. Sakamoto.

- Figures 46 to 49, 51 to 53: *Mexipyrus mojarrales* TAYLOR, spec. nov.
46, 47. Type, UMMZ 220192. Length 4.0 mm, width 2.4 mm, $5\frac{1}{2}$ whorls.
48, 49. Figured specimen, UMMZ 220193. Length 4.0 mm, width 2.4 mm, $5\frac{1}{2}$ whorls.
51. Figured specimen, UMMZ 220193. Length 3.9 mm, width 2.0 mm, $5\frac{3}{4}$ whorls.
52, 53. Figured specimen, UMMZ 220193. Length 3.7 mm, width 2.0 mm, 6 whorls.

- Figures 50, 54 to 57: *Mexipyrus multilineatus* TAYLOR, spec. nov.
50. Figured specimen, UMMZ 220198. Length 4.3 mm, width 2.3 mm, $6\frac{1}{4}$ whorls.
54. Type, UMMZ 220197. Length 5.2 mm, width 2.8 mm, $6\frac{1}{2}$ whorls.
55. Figured specimen, UMMZ 220198. Length 4.9 mm, width 2.2 mm, $6\frac{1}{2}$ whorls.
56, 57. Figured specimen, UMMZ 220198. Length 4.5 mm, width 2.2 mm, 6 whorls.

Explanation of Plate 19

Mexithauma quadripaludium TAYLOR, gen. et spec. nov. from the Valley of Cuatro Ciénegas, Coahuila.

Drawn by John Tottenham.

- Figures 58, 59: Figured specimen from Laguna Churince, UMMZ 220153. Length 7.7 mm, width 5.9 mm, $4\frac{1}{2}$ whorls.
Figures 60, 61: Figured specimen from Laguna Churince, UMMZ 220153. Length 6.6 mm, width 5.7 mm, $4\frac{1}{2}$ whorls.
Figures 62, 63: Type from Laguna Tío Candido, UMMZ 220214. Length 6.0 mm, width 5.25 mm, $4\frac{1}{2}$ whorls.



Figure 46



Figure 47



Figure 48

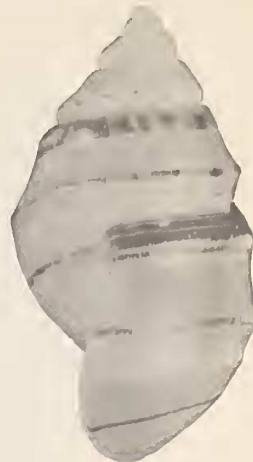


Figure 49



Figure 50



Figure 51



Figure 52



Figure 53



Figure 54



Figure 55



Figure 56



Figure 57

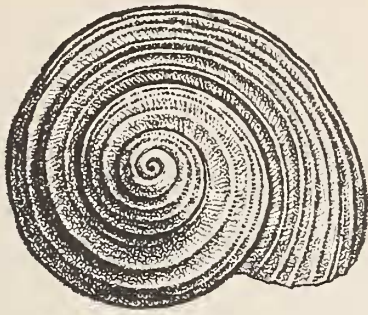


Figure 58

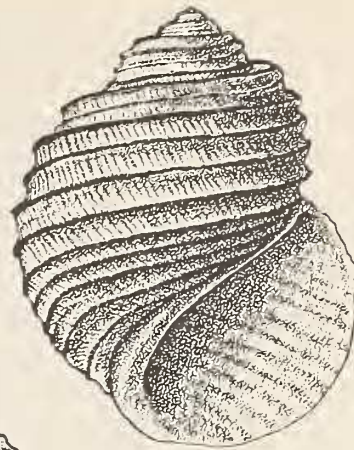


Figure 59



Figure 60



Figure 61



Figure 62

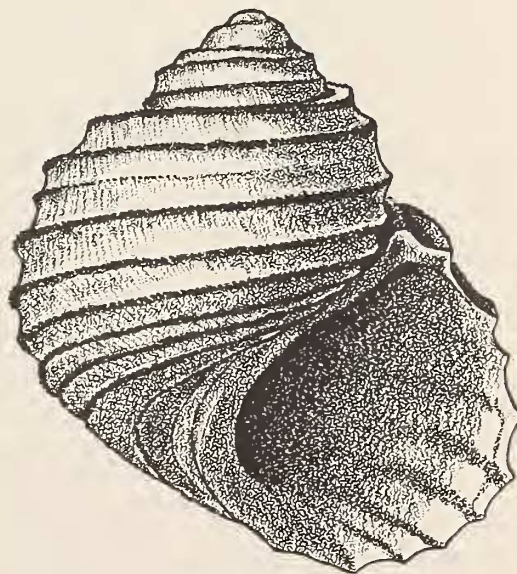


Figure 63

think it should be classified in the Micromelaniidae. Perhaps a rough or bristly periostracum will eventually turn out to be a significant, even if remote, link between *Antroselates* and *Mexithauma*.

Some other features of *Mexithauma* are certainly distinctive, but their taxonomic value is difficult to assess. The stripe along the dorsal surface of the tentacles is a feature I have not seen in any other Hydrobiidae, where the tentacles are either solidly pigmented, or have transverse bars of pigment, or an interior rod-like pigmented region. The numerous spiral cords on the shell are also unusual and might be significant. Sculpture in general is subdued in Hydrobiidae, and only one described genus of Hydrobiidae has numerous cords: *Rachipteron* THOMPSON (1964). Other features of this snail seem so different that I believe it is far better considered as one of the Rissoidae or Stenothyridae.

Mexithauma TAYLOR, gen. nov.

Diagnosis. Same as for the subfamily.

Type. *Mexithauma quadripaludium* TAYLOR, spec. nov.

Only the type species is included in the genus. It is known from several lagunas in the valley of Cuatro Ciénegas, Coahuila, México.

Etymology. The name is derived from México; and the Greek word *thauma*, *thaumatous*, a marvel or wonder: hence, a marvelous Mexican mollusk.

Mexithauma quadripaludium TAYLOR, spec. nov.

(Plate 19, Figures 58 to 63; Text figure 22)

Diagnosis. Same as for the genus and subfamily.

Type. UMMZ 220214. Coahuila, México: Laguna Tío Candido, 14 km south of Cuatro Ciénegas. D. W. Taylor, 15-IV-1965. Other specimens from the same collection are UMMZ 220215. The locality is number 8 on Text figure 2.

Localities and material examined (listed in geographic sequence around Sierra de San Marcos, beginning at the southwest).

Laguna Churince, 16 km SW Cuatro Ciénegas; D. W. Taylor, 12-IV-1965 (UMMZ 220153, figured specimens; 220152).

Pozos de la Becerra, 14 km SW Cuatro Ciénegas; C. L. Hubbs, 6-IV-1961 (UMMZ 220174); W. L. Minckley, 28-XII-1964 (UMMZ 220171); D. W. Taylor, 14-IV-1965 (UMMZ 220168).

West Laguna in El Mojarral, 1.7 km ENE of tip of Sierra de San Marcos; D. W. Taylor, 13-IV-1965 (UMMZ 220195).

East Laguna in El Mojarral, 1.9 km ENE of tip of Sierra de San Marcos; D. W. Taylor, 13-IV-1965 (UMMZ 220200).

¹¹ Laguna Escobeda, 12 km S of Cuatro Ciénegas; W. L. Minckley, 31-XII-1964 (UMMZ 220209); D. W. Taylor, 15-IV-1965 (UMMZ 220206).

¹² Laguna Tío Candido, 14 km S Cuatro Ciénegas; D. W. Taylor, 15-IV-1965 (UMMZ 220214, 220215).

General form, locomotion, behavior. The globose shell 6-8 mm long in adults is borne free of the substratum with the apex directed upward and posteriorly to the right, so that the axis of the shell forms an angle of about 45° with the long axis of the foot. In dorsal view when the snails are crawling the tip of the snout, and most of the length of the tentacles are visible in front of the shell. The posterior end of the foot and the eyes are not visible in this view, but the anterior corners of the foot may be seen as the snail turns from side to side. Compared to Hydrobiidae seen the snails crawl slowly. The animal cannot right itself when turned on its back.

The tentacles are thick at the base, taper to slender tips and are about ¾ the length of the shell aperture. The cilia are not arranged in a definite pattern. The tentacles are borne diverging at an angle of about 90°, and usually are in vertical or horizontal movement. They move both above and below a plane parallel to the substratum, and often touch the substratum as if sensing it. In crawling the snail keeps its snout appressed to the substratum, and moves it from side to side while browsing. The movement of the radula can be seen dimly within the snout.

Pigmentation. The ground color of the body is pale gray. The dorsal and lateral surface epithelium contains variably dense concentrations of fine melanin granules. Where dense, these granules form dark brown bands like those of the shell. Calcareous granules, much larger than the melanin granules, are conspicuous in the upper anterior parts of the body – in the front end of the foot, in the tentacles, and upper part of the rostrum. Here they lie beneath the surficial melanin granules and appear yellowish. Calcareous granules also are abundant in the mantle collar and posterior part of the body stalk, where they appear white and opaque.

The most heavily pigmented areas, appearing very dark brown, are the tentacles and the edges of the foot. The dorsal surface of the tentacles bears a diffuse-edged band of melanin, from nearly the tip posteriorly to just above the eye. Calcareous granules are scattered within the ten-

¹¹ Population extinct.

¹² Population studied from living specimens as well as relaxed, fixed material.

tacle, but there is no concentration around or behind the eyes, as is usual in Hydrobiidae.

The lower edges of the foot are heavily dusted with melanin granules that end sharply at the edge of the sole, thus forming a conspicuous lengthwise band. This band may be continuous around the hind end of the foot beneath the operculum, or broken up into variably dense patches. Anteriorly the band is wider and more diffuse on the front end of the foot.

The dorsal part of the head-foot is dusted with melanin, but less intensely than are the tentacles or edges of the foot. The melanin coats the dorsal and lateral surfaces of the snout, continuing posteriorly onto the back of the head and floor of the mantle cavity, and below the tentacular bases and eyes onto the upper sides of the foot. Melanin ends abruptly at the central side of the snout and below the eyes, so that the eyes are partly enclosed and set off by the pigmented area. The melanin becomes less dense and fades out gradually toward the anterior end of the snout, the upper surface of the tentacle bases, the sides of the foot, and within the mantle cavity. There are two areas thus left without melanin – a diffuse broad band on each side of the foot including the operculigerous lobe, and a small area around and above the eye in the bases of the tentacles.

The mantle collar is densely suffused with melanin, but mostly on the surface toward the shell and away from the observer looking into the mantle cavity. Thus the large calcareous granules in the collar stand out white in contrast.

The sole is pale gray, with a faint network of irregular, variably continuous darker gray melanin-pigmented areas within. These pigmented areas largely obscure the abundant translucent hyaline granules scattered in the tissue. **Head-foot mass.** The foot is not quite twice as long as wide. It is broadly rounded at the hind end, with gently convex sides, and 2 auriculate, mobile lobes at the anterior corners that are set off from the posterior part by a shallow constriction. An anterior pedal groove traverses the anterior edge of the foot.

The highly contractile snout is about $\frac{1}{3}$ as wide as the foot, flattened-oval in cross-section, and more convex dorsally. It tapers anteriorly more rapidly than in most Hydrobiidae seen. Two fleshy pads at the end of the snout together form a roughly oval area in anterior view, narrower dorsally. They are divided in the median plane by the slit of the mouth, and set off from the rest of the snout by a narrow constriction. The pads are pale gray and less translucent than adjacent parts of the snout. Unlike many Hydrobiidae studied, the pigment of the snout ends diffusely behind these pads, and not abruptly at their edges.

The eyes are in the lateral aspect of the bases of the tentacles. Their position differs from that usual in Hydrobiidae, in being closer to the base of the tentacle and within a low swelling less conspicuous than typical.

The mantle edge is not smooth, as in all other Hydrobiidae known, but bears low projecting papillae that fit into the grooves along the edge of the aperture, beneath the external ridges in the shell. No pattern of granules or pigment was correlated with the undulation of the mantle edge.

Verge (Text figure 22). The large verge fills most of the mantle cavity in the male. The broad insertion is transverse, from a little to the left of the median plane to

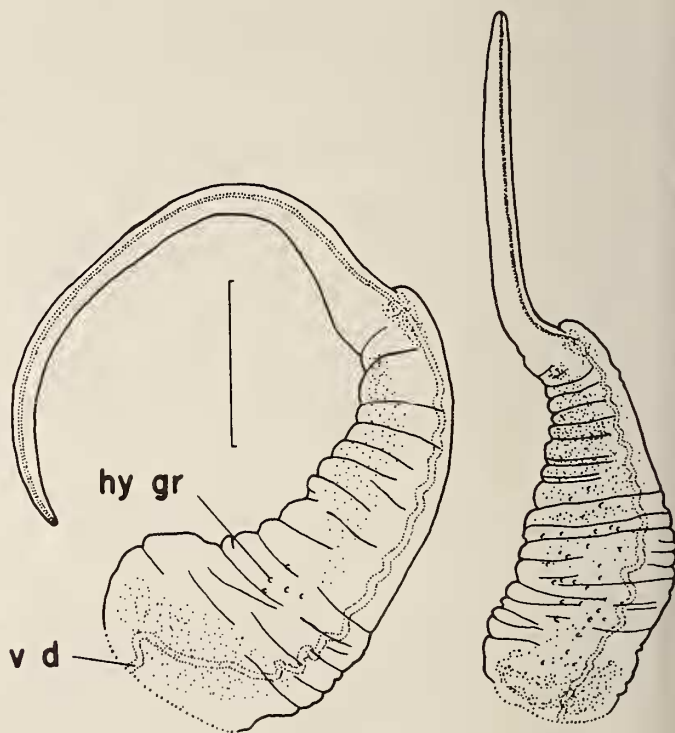


Figure 22

Verges of *Mexithauma quadripaludium* TAYLOR, gen. et spec. nov., dorsal view. Scale line = 1 mm. hy gr - hyaline granule; v d - vas deferens.

a sagittal plane through the base of the right tentacle. The broad proximal part is curved to the left and ordinarily carried so that it ends shortly within the aperture. The slender distal part extends posteriorly into the mantle cavity from an "elbow" where it originates on the proximal part of the verge. The distal part may be carried straight, or coiled through 360° , but the tip of

the verge ordinarily points to the rear of the mantle cavity.
Etymology. The name *quadripaludium* is the Latin translation of "de las cuatro ciénegas" or "of the four marshes."

HYDROBIIDAE?

Paludiscalinae TAYLOR, new subfamily

Diagnosis. Shell turritiform, about 2.1 - 2.5 mm long, 1.0 to 1.2 mm wide, with $6\frac{1}{2}$ - $7\frac{1}{2}$ whorls ovate in cross-section and separated by a deeply incised suture. Sculpture consists of opisthocyrt lamelliform costae, about 12 per whorl, that are crescentic in profile and highest on the shoulder of the whorl. Base narrowly phaneromphalous. Aperture ovate, in adult shells simple, with no flare of outer lip or callus inside; simply adnate to preceding whorl. Apex blunt; protoconch of 1 whorl, smooth.

Referred genera. *Paludiscala* TAYLOR, gen. nov., is the only included genus.

Discussion. The spectacular little snails described here as *Paludiscala*, gen. nov., obviously represent a distinctive group within a known family, or even a new family. At first sight they are strikingly like Epitoniidae, on account of the white color, turritiform shape and widely spaced lamelliform costae. Epitoniidae are all marine, several times as large as *Paludiscala*, and usually have whorls more nearly circular in cross-section.

Another group that is slightly reminiscent of *Paludiscala* is Truncatellidae, a group of snails living on land, either inland or above high-tide mark. They are closer in size to *Paludiscala* than are Epitoniidae, but in all known

genera the apex is broken off and the upper end of the shell plugged with a limey deposit.

The size, shape, and inland habitat lead me to think the genus is one of the Rissoacea, but until the anatomy is known, no precise allocation will be possible.

Paludiscala TAYLOR, gen. nov.

Diagnosis. Same as for the subfamily.

Type. *Paludiscala caramba* TAYLOR, spec. nov.

Only the type species is included in the genus. It is known only from the type locality, in the valley of Cuatro Ciénegas, Coahuila, México. Even the habitat is uncertain, as the snails might live either in wet places in the marshes, or in the springs proper.

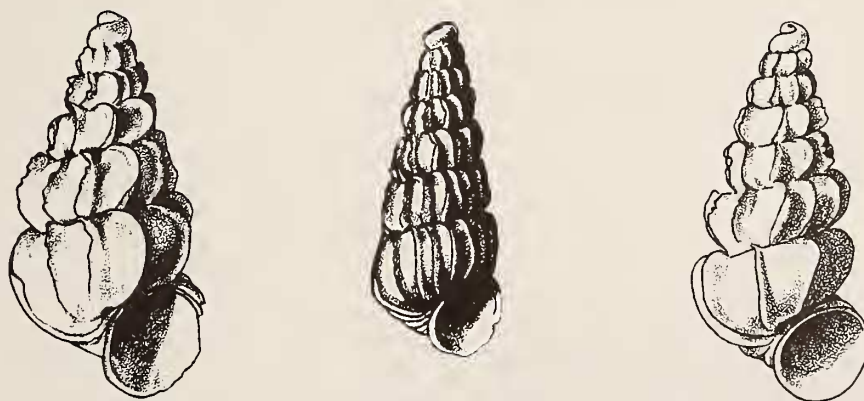
Etymology. The name is from the Latin words *palus*, *paludis*, a marsh; and *scala*, literally a staircase, in reference to the generic name *Scala*, by which many Epitoniidae were once known.

Paludiscala caramba TAYLOR, spec. nov.

(Plate 13, Figures 11, 14, 16; Text figures 23 to 25)

Diagnosis. Same as for the genus and subfamily.

Type. UMMZ 220164. Coahuila, México: spring tributary to the area of marshes and lagunas named "El Mojarral," 1.7 km due east of the northern tip of Sierra de San Marcos, 11 km southwest of Cuatro Ciénegas. W. L. Minckley, 13-IV-1965. The same collection yielded 18 other specimens; 2 of these are figured (UMMZ



Figures 23 to 25

Paludiscala caramba TAYLOR, gen. et spec. nov.

Figure 23: Figured specimen, UMMZ 220165. Length 2.6 mm; width 1.4 mm; $6\frac{3}{4}$ whorls.

Figure 24: Figured specimen, UMMZ 220165. Length 2.3 mm; width 0.9 mm; $7\frac{1}{4}$ whorls.

Figure 25: Type, UMMZ 220164. Length 2.5 mm; width 1.2 mm; $7\frac{1}{2}$ whorls.

220165), 16 unfigured (UMMZ 220163). The locality is number 1 on Text figure 2.

Material. The collection came from the soft black organic mud of a small spring, where *Durangonella* sp. was abundant. None of the snails, either *Paludiscala* or *Durangonella*, was alive, nor freshly dead so as to retain traces of the body, or operculum. Many of the *Durangonella* retain the periostracum, and only a few are bleached chalky white, as are all specimens of *Paludiscala*. If *Paludiscala* lived along with *Durangonella* in this spring, then probably it has a thinner periostracum, or virtually none.

Variation. The chief variation is in length/width ratio, and strength and spacing of costae. Size, cross-section of whorl, and apertural characters are more constant. The extremes of width are 1.0 and 1.2 mm, both found in shells 2.1 mm long. The figured specimens were selected to show variation in both shape and in sculpture.

The costae are not arranged in a consistent pattern, and their number per whorl does not even increase regularly with growth. The number on the body whorl is 11-16; on the preceding whorl, 9-14; and on the one before that, 7-16. Generally the number of costae on a given whorl is greater than that on the preceding whorl, but even this is not invariable.

A common variation in spacing and strength of costae occurs in the first and last quarter-whorls of the teleoconch. The smooth protoconch (with no sculpture evident at 50x magnification) is set off from the teleoconch by costae that are lower and more closely spaced in the first quarter-whorl of post-embryonic growth than later. Similarly, costae on the last quarter-whorl of the body whorl are more crowded and lower than previously. This is the only evidence of determinate growth; there is no descent of the suture, loosening of the body whorl, apertural callus, or terminal flare of the aperture as in some Rissoacean snails.

Etymology. ¡caramba!, an exclamation, loosely translated from my original remarks at seeing the shells. An epitoniid-like snail in the arid interior of northern México is thoroughly implausible.

ASSIMINEIDAE

Assiminea FLEMING, 1828

Assiminea sp.

Five specimens (UMMZ 220176), all but one worn and lacking periostracum, were found in a bottom sample from the northernmost pool of Pozos de la Becerra, 14 km southwest of Cuatro Ciénegas, collected by C. L. Hubbs, 6-IV-1961. The species is almost certainly new, but I defer description in the hope of obtaining more material in better condition, hopefully alive. Most species of Assi-

mineidae are at least semiterrestrial, so that this Mexican species probably lives in wet marshy areas around the spring-pools, not in the springs proper. This habitat has never been searched by a malacologist in the Cuatro Ciénegas valley, and hence there is hope for finding *Assiminea* there alive.

In America the species of Assimineidae are few compared to the number in eastern Asia, and they are best known from near high-water mark along the coast, or in salt marshes. The only inland occurrences of *Assiminea* previously recorded in North America are in the Death Valley region of southeastern California, U. S. A. S. S. BERRY (1947) described *A. infima* from "Bad Water," the salt-saturated pool below sea level that is the lowest point on the continent. MORRISON (1956) has suggested another species lives around Saratoga Springs, at the south end of Death Valley.

Still another undescribed species of *Assiminea* of inland habitat is represented in U. S. Geological Survey collections from Panamint Valley, Inyo County, California. This valley is the one next west from Death Valley, and like Death Valley it has scarcely been explored by a malacologist. Hence there is a real possibility that *Assiminea* still lives there. Precise locality data for the fossil occurrence are as follows:

U. S. Geological Survey Cenozoic locality M2617. Inyo County, California. Panamint Butte quadrangle (1951) 1:62500, 1000 feet east, 700 feet south of northwest corner, sec. 14, T. 18 S., R. 42 E. Archeological site Iny-19, from within and below organic mat dated 10520 ± 140 years B. P. (UCLA-990), about six feet below surface in bulldozer trench exposure. Collected by E. L. Davis, University of California at Los Angeles.

In the light of these inland occurrences in southwestern California and central Coahuila, one may suppose *Assiminea* will be found at other places in the scarcely known interior of northern México.

Species of *Assiminea* are most diversified in eastern Asia. In addition to the small, plain, brown-shelled forms that ABBOTT (1958) called the "nitida-complex" (including all the American species) there are larger, more sculptured species and some with color bands. This greater morphological diversity is not correlated with greater ecological range than in America. ABBOTT (1958) found that in the Philippines *Assiminea* is a coastal and brackish-water group. One species, *A. thielei*, lives in fresh water most of the year and will not tolerate submersion in saline waters; it is the most nearly freshwater species in the region. In New Guinea JUTTING (1963) noted that one species, *A. riparia*, had the unusual habit of living on the bank of a freshwater lake; other species in the area live in brackish-water and coastal habitats.

BASOMMATOPHORA

LYMNAEACEA

LYMNAEIDAE

Fossaria WESTERLUND, 1885*Fossaria obrussa* (SAY, 1825)

PILSBRY (1904: 777) recorded "*Limnaea desidiosa* SAY" from Saltillo, Coahuila. The record was assigned by F. C. BAKER (1911) to *Fossaria obrussa*, perhaps the most widely distributed lymnaeid in North America.

ANCYLACEA

ANCYLIDAE

Gundlachia PFEIFFER, 1849*Gundlachia excentrica* (MORELET, 1851)

One empty but well preserved shell is identified as this species in the sense of WALKER (1903), both from that paper and comparison of specimens. The species is known from southern Texas, U. S. A., southward to Guatemala.

Assignment of the species to *Gundlachia* is based on the conclusions of HARRY & HUBENDICK (1964), who included the West Indian *Gundlachia radiata* (GUILDING) within the genus. That species was recognized as similar to *G. excentrica* (MORELET) by WALKER (1903), and the 2 were even synonymized by WURTZ (1951). BASCH (1963) assigned the species to *Hebetancylus*.

Locality and material examined. Coahuila, México: Río Salado de los Nadadores at El Cariño de la Montaña, 20 km east of Cuatro Ciénegas; D. W. Taylor, 12-IV-1965 (UMMZ 220148).

PLANORBIDAE

The primary work on Planorbidae is that by F. C. BAKER (1945); Mexican locality data therein have been indexed by DRAKE (1948). More recent work on tropical American Planorbidae is accessible through papers by HARRY (1962) and HARRY & HUBENDICK (1964).

Drepanotrematinae?

Drepanotrema CROSSE & FISCHER, 1880?

Three tiny shells (UMMZ 220179), all broken and lacking periostracum, may belong to the genus *Drepano-*

trema. They are tightly coiled, planispiral, and more like *Drepanotrema* than *Gyraulus*, *Antillorbis*, *Promenetus*, or other small Planorbidae that might occur in the region. The specimens were in a bottom sample from the northernmost pool of Pozos de la Becerra, 14 km southwest of Cuatro Ciénegas, collected by C. L. Hubbs, 6-IV-1961.

Helisomatinae

Helisoma SWAINSON, 1840*(Helisoma)* s. s.*Helisoma* (s. s.) *anceps* (MENKE, 1830)

Specimens found in a spring beside Río de los Nadadores, at El Cariño, are typical of the widespread creek form of the species, and show no differences worthy of taxonomic separation. The nearest records are in the spring-fed streams along the edge of the Balcones Escarpment, in central Texas. Suitable habitats for the species are doubtless sparse in the arid regions of northern México and the southwestern United States, so that its distribution is widely discontinuous. MILSTEAD (1960) summarized the distribution of some amphibians whose range is similarly discontinuous in the region. Perhaps some of their ranges may prove closely similar to that of *Helisoma anceps* when more mollusk collections are known.

In summarizing the distribution of this species, WALKER (1909) found it is widespread throughout central and eastern North America, and occurs sparsely in the Pacific Northwest. He doubted the record in Sonora, at the mouth of the Yaquí River, but F. C. BAKER (1945: 402 to 403) illustrated a specimen from that locality. This was the only previously known occurrence of *Helisoma anceps* in México.

Specimens: UMMZ 220146.

PHYSACEA

PHYSIDAE

Physa DRAPARNAUD, 1801*(Physella)* HALDEMAN, 1842

The original criteria for establishment of *Physella* were trivial, as noted by F. C. BAKER (1928: 416), but the name is the earliest one applicable to the group of species with an acute (not rounded) apex, and mantle unreflected over the outer lip. MARTENS (1890-1901: 368) evidently had much the same group in mind when he proposed *Alampetis* (preoccupied). At least in the present state of knowledge I see no reason to recognize 2 separate sub-

groups, so that *Alampetis* MARTENS (1898), *non* THOMSON (1878), and *Alampetista* ZILCH (1956) are included as synonyms.

In identifying the specimens I have from Coahuila, and in dealing with the literature of *Physa* from the region, I have reviewed long series of specimens from the southwestern U. S. A. and northern México. Thanks to considerable field work in the region, as well as extensive material, I have been able to see both type material as well as the range of variation encountered in a variety of habitats. No classification in this genus can be based satisfactorily on shell characters alone, but this is all the previous species have been based on and I have simplified the group and put it on a slightly firmer foundation.

The following forms have been named from southwestern U. S. A. and northeastern México:

Physa humerosa GOULD, 1855, Proc. Boston Soc. Nat. Hist. 5: 128. "Colorado Desert [California] and at Pecos River [New Mexico or Texas]." GOULD, 1857, Rep. U. S. Explorations and surveys for a railroad route . . . to the Pacific Ocean, 5 (2): 331, pl. 11, fig. 1 - 5. Type ANSP 17279 (H. B. BAKER, 1964), figured by BINNEY (1865: 92, text-fig. 157). JOHNSON (1964) lists syntypes only from MCZ and USNM collections. In none of these publications is a restricted type locality clear; it is designated here as the Colorado Desert, California.

Physa virgata GOULD, 1855, Proc. Boston Soc. Nat. Hist. 5: 128. "River Gila [Arizona], and near San Diego [California]." Type ANSP 17244a (H. B. BAKER, 1964). Lectotype MCZ 72995 (JOHNSON, 1964; the locality San Francisco is an error for San Diego). Perhaps neither one of these type specimens has a precise locality; if so it has not been published. JOHNSON (1964, pl. 44, fig. 5) illustrated the MCZ lectotype.

Physa traskii LEA, 1864, Proc. Acad. Nat. Sci. Philadelphia 16: 115. "Rio Los Angeles, California." LEA, 1867, Observations on the genus *Unio* . . . , 11: 119, pl. 24, fig. 80.

Physa osculans rhyssa PILSBRY, 1899, Proc. Acad. Nat. Sci. Philadelphia 51: 401. Saltillo, Coahuila, México. Type ANSP 77218a (H. B. BAKER, 1964).

Physa virgata alba COCKERELL, 1902, Journ. Malac. 9: 138. Salt River at Tempe, Arizona. Not of CRANDALL, (1901).

Physa bottimeri CLENCH, 1924, Nautilus 38: 12, text-fig. 4. Comanche Spring, Fort Stockton, Pecos County, Texas.

Physa marci F. C. BAKER, 1924, Nautilus 38: 15, text-fig. 5. Little Valientia Spring, Santa Barbara National Forest, California. The type locality has not been precisely recovered; I cannot find a "Santa Barbara National Forest" nor a spring of that name in the vicinity of Santa Barbara.

Physa humerosa interioris "FERRISS" PILSBRY, 1932,

Nautilus 45: 139, pl. 11, fig. 12. West branch of Navajo Creek, Coconino County, Arizona. The name as published originally by FERRISS (1920) is nude, hence it should be credited to PILSBRY as done by H. B. BAKER (1964).

The species of *Physa* in this region can be grouped conveniently into 2 species-groups. In one group the shell attains a larger size, the spire is shorter, and the body-whorl is characteristically shouldered. The work by SPRINGER (1902) indicates some radular differences, but not enough species have been investigated to judge what characters are significant. This is the *lordi*-group of F. C. BAKER (1928: 424). The second group includes species that attain a smaller size, have a shell with longer spire, and are characteristically not shouldered. This may be called the *gyrina*-group after its most widespread species; most *Physella* fall into this species-group.

Group of *Physa gyrina*

In previous work (HIBBARD & TAYLOR, 1960: 115 - 121) on *Physa* in the Great Plains region of the United States I recognized that shells of the subgenus *Physella* could be sorted into 2 categories: (a) shells usually larger, with a conspicuous and usually thicker apertural callus, and shorter spire with shallower sutures; more northern in distribution, identified as *Physa gyrina* SAY; (b) shells usually smaller, with a less conspicuous, thinner apertural callus, and longer spire with deeper sutures; more southern in distribution, identified as *Physa anatina* LEA. Since that time I have studied material from more western and southern areas, and collected in a variety of habitats in parts of México and U. S. A. From this experience I find that these same differences hold true from the Great Plains westward to the Pacific Ocean: commonly there is a larger, shorter-spined *Physa* to the north, and a smaller, higher-spined form, often with deep sutures, to the south. The oldest name surely applicable to this southern form is *P. virgata* GOULD (1855). I have reviewed specimens of *Physa* from southern California eastward to Kansas and southward to Texas and México, and examined nearly all the pertinent types, but have not tried to revise the scattered published records from the region.

Physa (Physella) virgata GOULD

(Plate 14, Figure 18)

In springs and small perennial streams from southern California to trans-Pecos Texas the *Physa* is usually only 8 to 10 mm long, with an aperture $\frac{2}{3}$ - $\frac{3}{4}$ of the shell length, deep sutures, narrow spire, no shoulder on the body whorl, and no apertural callus. This form is regionally so

similar that surely there is no warrant for recognizing more than one species. With increasing size of the water body the shells may grow larger, and especially in slow-moving streams or ponds they become more swollen. *Physa humerosa interioris* PILSBRY (1932), from Arizona, the *Physa* from New Mexico illustrated by SPRINGER (1902), and *P. traskii* LEA (1864) are of this slightly larger stream form. The formation of an apertural callus is irregular; often there is none at any age. In none of this variation is any geographic pattern evident.

Specimens from northeastern Mexico are scarce in museum collections. UMMZ 123599 includes 4 specimens marked "Cotypes" of *Physa osculans rhyssa* PILSBRY (1899) from Saltillo, Coahuila. These seem to me to be only long-spined shells of *P. virgata*. They can be duplicated at other localities to the north, for example by a larger series (UMMZ 176787) from Old Log Spring, west of The Solitario, Presidio County, Texas, collected by Leslie Hubricht, 30-V-1938. The riblets mentioned by PILSBRY are often found on *Physa*, presumably because of irregular growth in later life, and are not even restricted to *P. virgata* in the broad sense used here. Three lots (UMMZ 122115, 122121, 123600) from Valles, San Luis Potosí, México, collected by A. A. Hinkley, all fall within the range of *P. virgata* to the north, but were labelled *P. osculans*, *P. osculans rhyssa*, and *P. mexicana*. From study of the variation in *Physa* found in different habitats within a small area, I see no evidence for 3 species here, and they are all closer to *P. virgata* in form than to specimens from central México.

In Coahuila thus there seems to be no evidence of more than one *Physa*, *P. virgata*. The record by DALL (1905: 193) of *Physa berendti* DUNKER also is based on *P. virgata* (specimens USNM 110403). The locality "Twenty-five miles southeast of Saltillo" is at least close to the southeastern border of Coahuila, and might be inside that state.

As one traces the variation and distribution of *Physa virgata* eastward from New Mexico and trans-Pecos Texas the shells are commonly larger (15 mm is frequent) and several irregularly spaced apertural thickenings are common, appearing as white collabral bands through the shell. These represent the species I have previously (HIBBARD & TAYLOR, 1960; TAYLOR, 1960) called *Physa anatina* LEA; but there are no reliable shell characters to distinguish it from the southwestern *P. virgata*. The difference in the regional variation I think could be accounted for entirely by differences in the suitable habitats available, but only anatomical studies can resolve this question.

Physa rhomboidea CRANDALL (1901) was described in part from specimens from Las Vegas, New Mexico; the type locality is Muddy Creek, Sedalia, Pettis County,

Missouri, U. S. A. The Las Vegas specimens I agree with SPRINGER (1902) are *P. virgata*. The syntypes (originally 40775 of Bryant Walker collection) are UMMZ 130515, and as between *P. gyrina* and *P. virgata* are certainly the latter. A revision of *Physa* in this area is beyond the scope of this study, and other species perhaps distinct from the 2 common western ones should be considered.

In southernmost Texas, around Brownsville, occurs a form that might be an extreme variant of *Physa virgata*, or a distinct species. The shells attain a length of 20 mm, longer than any others seen from the range of *P. virgata*, but are narrow and high-spined as in *P. virgata*.

Physa marci F. C. BAKER (1924) from California is probably an ecologic variant of *P. virgata*, but I have not seen either the original material nor topotypes. *Physa virgata* is otherwise the only species in coastal southern California.

Summary of distribution. *Physa virgata* is common over most of south-central and southwestern North America. In California it is found at least as far north as Sacramento and San Francisco Bay, and extends thence into northernmost Baja California and eastward. It occurs in southernmost Nevada, southernmost Utah, and Colorado, but northward is replaced by *P. gyrina*. In southern Kansas, and southward perhaps throughout Texas, *P. virgata* is the only living species of the genus. Its range extends eastward an unknown extent; and southward over most of the Mexican Plateau.

Comparison with species from México. Only 2 names published prior to *Physa virgata* GOULD (1855) have sometimes been applied to specimens of that species. These are *Physa osculans* HALDEMAN and *P. mexicana* "PHILIPPI" KÜSTER; references to literature and illustrations are accessible through the work by MARTENS (1890 to 1901). Neither of the 2 species was described from a locality more precise than "Mexico"; and in a group so variable as *Physa* one may doubt whether they can be recognized.

USNM 543500 is a single fossil specimen from a peat bed near the village of Tepexpam, Lake Texcoco, D. F., México, collected by A. R. V. Arellano. Its large size, short spire, shallow sutures, and relatively thick shell are features distinct from *Physa virgata* and like those of *P. gyrina*. The specimen could readily be matched in late Pleistocene assemblages from the central United States. This example is significant in confirming the authenticity of Recent specimens with shells like *P. gyrina* from this part of México.

USNM 9009 includes 3 Recent shells identified as "*Physa osculans* HALD. Mexico. A.N.S." They were listed under that name by BINNEY (1865: 83). Lacking a precise locality, they are of value mainly in showing what

was taken as *P. osculans* in that day, but might have been identified by Haldeman and be part of the original lot. These shells are distinguished from *P. virgata* by larger size, and shallower sutures, but in height of spire are not diagnostic. One short-spined specimen is like *P. gyrina*, but the other two are not characteristic in this respect.

UMMZ 123391 is from Tlalpan, near México, D. F., collected by S. N. and M. C. Rhoads, 1899, and labelled *Physa osculans* HALDEMAN. The specimens are short-spined with shallow sutures, and if they were labelled as coming from Ohio or Idaho, for example, I would call them *P. gyrina*. They agree well with the figures of *P. mexicana* published both by MARTENS and KÜSTER, but not so closely with the type of *P. osculans*. At any rate there seems to be a typical *Physa* other than *P. virgata* in central México. Perhaps *P. virgata* and *P. osculans* are one species, but in the absence of a precise type locality I do not see how to establish this. The illustration of the type of *P. osculans* (HALDEMAN, 1840-1844, 6: pl. 2, fig. 11) might be *P. virgata* or *P. mexicana*. In the interest of stability of nomenclature and clarity of understanding, the name *P. osculans* might best be ignored, or at least not used for *P. virgata*.

Localities and material examined (Coahuila only).

Rancho San Marcos, 20 km SSW Cuatro Ciénegas; D. W. Taylor 14-IV-1965 (UMMZ 220217) (Plate 14, Figure 18).

Río Mesquites, 9 km SW Cuatro Ciénegas; D. W. Taylor, 13-IV-1965 (UMMZ 220191).

Río Salado de los Nadadores, El Cariño de la Montaña, 20 km E Cuatro Ciénegas; D. W. Taylor, 12-IV-1965 (UMMZ 220147).

Saltillo; S. N. and M. C. Rhoads, 1899 (UMMZ 123599; USNM 160166; paratypes of *Physa osculans rhyssa* PILSBRY).

Twenty-five miles southeast of Saltillo; E. Palmer (USNM 110403).

Physa (Physella) virgata bottimeri CLENCH, 1924
CLENCH (1924) described *Physa bottimeri* from 4 specimens. Two of these I have studied: the holotype (UMMZ 31617) and a paratype (UMMZ 117581) collected by L. J. Bottimer, 14-I-1922, at Comanche Spring, Fort Stockton, Pecos County, Texas. The specimens are markedly distinct by the strongly shouldered body whorl, short spire, and apertural callus.

Two series of topotypes (UMMZ 132522, 132523) collected by C. L. Hubbs, 1938, substantially blur the

distinctiveness of this form. They include both typical *Physa virgata* and forms intermediate between *P. virgata* and *P. bottimeri*. Whether they are only an ecological form or a genetically differentiated relative of *P. virgata* is undeterminable; the type locality has been destroyed and there is no longer a spring there. On account of these annectant forms I am lowering the rank of *P. bottimeri* to subspecies. On account of its distinctiveness it would be unwarranted to relegate it to the synonymy of *P. virgata* as yet.

Four small, immature specimens (UMMZ 66335) are unusual in having incipient shoulders to the body whorl despite their size, and might have grown into shells much like *Physa bottimeri*. They are from the "head spring at Toyahvale, Reeves Co., Texas"; perhaps study at this locality might shed light on *P. bottimeri*.

Group of *Physa lordi*

In the southwestern U. S. A. at least 2 species belong to this group: *Physa humerosa* GOULD, and an undescribed species mentioned by SPRINGER (1902) from the Organ Mountains, New Mexico. *Physa humerosa* I consider restricted to southeastern California, southwestern Arizona, and adjacent Baja California. It is most widely represented in museum collections by subfossil specimens from the Colorado Desert, California, where it is now extinct. The only specimens collected alive that I have seen are USNM 29119, 2 shells fresh and retaining periostracum, labelled "Gila River, Arizona;" they were collected by a Dr. Loew, in 1873.

Physa patzcuarensis PILSBRY (1891 a), from Lago Patzcuaro, Michoacán, México, might possibly belong to this group; if so it is the most southerly representative. Although described as a variety of *P. osculans*, it seems deserving of specific rank.

STYLOMMATOPHORA

SUCCINEACEA

SUCCEINIDAE

One broken shell (UMMZ 220155), presumably representing *Catinella* or *Succinea*, was screened from the bottom of the outflow of Laguna Churince. It is the only land snail collected so far in the valley of Cuatro Ciénegas. At this locality no search was made for snails except in water, so live Succineidae can probably be found here.

TAXONOMIC AND NOMENCLATURAL CHANGES

NEW CATEGORIES AND NEW RANKS

HYDROBIIDAE

Cochliopinae, new subfamily, with 3 tribes

Cochliopini, new rank (= Cochliopinae TRYON, 1866), for *Cochliopina* STIMPSON (1865), *Cochliopina* MORRISON (1946), *Lacunorbis* YEN (1950), *Limnothauma* HAAS (1955), *Nanivitreia* THIELE (1927), and *Subcochliopa* MORRISON (1946).

Cochliopina milleri TAYLOR, spec. nov.

Horatiini, new tribe, for *Coahuilix* TAYLOR, gen. nov.; *Gocea* HADŽIŠČE (1956a); *Hadziella* KUŠČER (1932); *Horatia* BOURGUIGNAT (1887), including the subgenera *Horatia s.s.*, *Daudebardiella* BOETTGER (1905), *Hauffenia* POLLONERA (1898) and *Neohoratia* SCHÜTT (1961); *Lyhnidia* HADŽIŠČE (1956b); *Ohridohoratia* HADŽIŠČE (1956b), including the subgenus *Ohridohauffenia* HADŽIŠČE (1956b); and *Ohrigocea* HADŽIŠČE (1956b), including the subgenus *Karevia* HADŽIŠČE (1956b).

Coahuilix hubbsi TAYLOR, gen. et spec. nov.

Clenchiellini, new tribe, for *Clenchiella* ABBOTT (1948)

Fontigentinae, new subfamily, for *Fontigens* PILSBRY (1933)

Lithoglyphinae, new subfamily, for *Lithoglyphus* HARTMANN (1821)

Littoridininae, new subfamily, for *Brachypyrghulina* HAAS (1955), *Durangonella* MORRISON (1945), *Ecpomastrum* HAAS (1957), *Heligmopoma* HAAS (1955), *Idiopyrgus* PILSBRY (1911), *Littoridina* SOULEYET (1852), *Littoridinops* PILSBRY (1952), *Lyrodes* DOERING (1884), *Mexipyrghus* TAYLOR, gen. nov., *Pyrgophorus* ANCEY (1888), *Rhamphopoma* HAAS (1955), *Strombopoma* HAAS (1955), *Texadina* ABBOTT & LADD (1951), *Tryonia* STIMPSON (1865), and *Zetekina* MORRISON (1947).

Durangonella coahuilae TAYLOR, spec. nov.

Mexipyrghus carranzae TAYLOR, gen. et spec. nov.

M. churinceanus TAYLOR, spec. nov.

M. escobedae TAYLOR, spec. nov.

M. lugoi TAYLOR, spec. nov.

M. mojarralis TAYLOR, spec. nov.

M. multilineatus TAYLOR, spec. nov.

Nymphophilinae, new subfamily, for *Nymphophilus* TAYLOR, gen. nov.

Nymphophilus minckleyi TAYLOR, gen. et spec. nov.

HYDROBIIDAE?

Mexithaumatinae, new subfamily, for *Mexithauma* TAYLOR, gen. nov.

Mexithauma quadripaludium TAYLOR, gen. et spec. nov.

HYDROBIIDAE?

Paludiscalinae, new subfamily, for *Paludiscala* TAYLOR, gen. nov.

Paludiscala caramba TAYLOR, gen. et spec. nov.

TAXONOMIC CHANGES

VALVATACEA

VALVATIDAE

Carinulorbis utahensis LAROCQUE, 1960 = *Valvata bicincta* WHITEAVES, 1885

VIVIPARACEA

Bithyniidae are transferred from Rissoacea

RISSEOACEA

STENOTHYRIDAE, or RISSOIDAE (Stenothyridae)

Rachipteron THOMPSON, 1964 is transferred from HYDROBIIDAE

HYDROBIIDAE

Amnicolinae

Hydrobia greggi PILSBRY, 1935, is assigned to *Amnicola*

Cochliopinae

"*Planorbis*" *bourguyi* ROXO, 1924; "*Planorbis*" *pebasana* CONRAD, 1874; and "*Planorbis*" spec. of DE GREVE, 1938, are probably Cochliopinae instead of PLANORBIDAE

Carinulorbis YEN, 1946, non CONRAD, 1862 = *Carinulorbis* YEN, 1949, is synonymized with *Clenchiella* ABBOTT, 1948

Valvata kugleri FORCART, 1948, is assigned to *Cochliopina*

Littoridininae

Hydracme HAAS, 1938 = *Idiopyrgus* PILSBRY, 1911

Isaea CONRAD, 1871 = *Tryonia* STIMPSON, 1865

Liris CONRAD, 1871 = *Tryonia* STIMPSON, 1865

Dyris CONRAD, 1871 = *Tryonia* STIMPSON, 1865

Conradia WENZ, 1925 = *Tryonia* STIMPSON, 1865

Potamopyrgus amazonicus HAAS, 1949 is assigned to *Tryonia*

Potamopyrgus? bakeri PILSBRY, 1891 is assigned to *Tryonia*

Pyrgulopsis blakeana TAYLOR, 1950 = *Tryonia protea* (GOULD)

Pyrgulopsis cahuillorum TAYLOR, 1950 = *Tryonia protea* (GOULD)

Potamopyrgus cheatumi PILSBRY, 1935, is assigned to *Tryonia*

Calipyrgula circumstriata LEONARD & HO, 1960 b is assigned to *Tryonia*

Paludestrina curta ARNOLD, 1903 = *Tryonia imitator* (PILSBRY)

Potamopyrgus fagundes HAAS, 1938, is assigned to *Tryonia*

Calipyrgula hibbardi LEONARD & FRANZEN, 1944 is assigned to *Pyrgophorus*

Paludestrina imitator PILSBRY, 1899 d is assigned to *Tryonia*

Potamopyrgus laciranus PILSBRY & OLSSON, 1935 is assigned to *Tryonia*

Pyrgulopsis? patzcuarensis PILSBRY, 1891, is assigned to *Tryonia*

Calipyrgula pecosensis LEONARD & HO, 1960 a is assigned to *Tryonia*

Hydrobia reevii FRAUENFELD, 1863, is assigned to *Pyrgophorus*

Calipyrgula senta LEONARD & FRANZEN, 1944, *C. tumida* LEONARD & FRANZEN, 1944, and *C. turricula* LEONARD & FRANZEN, 1944 = *Pyrgophorus hibbardi* LEONARD & FRANZEN, 1944

Lyrodes hertleini DRAKE, 1956, is *incertae sedis*, probably not Littoridininae

MICROMELANIIDAE

Antroselates HUBRICHT, 1963, is transferred from HYDROBIIDAE

ANCYLACEA

ANCYLIDAE

Ancylus excentricus MORELET is assigned to *Gundlachia*

PHYSACEA

PHYSIDAE

Physa osculans rhyssa PILSBRY, 1899 = *P. virgata* GOULD

Physa anatina LEA, 1864 = *P. virgata* GOULD

Physa marci F. C. BAKER, 1924, probably is a synonym of *P. virgata* GOULD

Physa bottimeri CLENCH, 1924 is lowered to subspecific rank as *P. virgata bottimeri*

Physa osculans patzcuarensis PILSBRY, 1891, is raised to specific rank

SUMMARY

The small valley of Cuatro Ciénegas, about 30 by 40 km, in central Coahuila, northeastern México, has yielded the most spectacularly endemic fauna of freshwater snails known in the Western Hemisphere. The scanty collecting so far has been concentrated on only one habitat, the large springs, so that doubtless future additions will be made. Out of about 18 forms, only 13 can be identified specifically. One species is widespread in the region; the other 12 are new endemic species classified in five new endemic genera of which three represent new endemic subfamilies. This remarkably localized fauna shows scarcely any resemblance to known mollusks of eastern México, but the interior plateau of México is so poorly known that perhaps some groups will turn up elsewhere. Recent intensive development of the springs for irrigation has already exterminated some populations, perhaps a few species, and threatens many others in the immediate future.

The nearest parallel in the Western hemisphere to the localized endemism of the Cuatro Ciénegas valley is in Lake Titicaca, Bolivia - Peru. Five genera are restricted to this lake, and another nearly so; all belong to widespread subfamilies and are not isolated taxonomically like the striking endemics in México.

Besides being strongly differentiated from the taxonomic standpoint, four of the new endemic genera are unusual morphologically. In having elaborate sculpture, color banding, a bristly surface, or being of large size for their groups they remind one more of marine snails than the groups to which they are anatomically similar.

Out of five localized new genera, three are known only by shells from one locality each. The other three genera were collected alive at several localities, where they occur as isolated populations showing different degrees of morphological divergence. Two of the genera are not differ-

entiated morphologically, but *Mexipyrus* has undergone remarkable divergence. Seven populations sampled are assigned to six species. The morphological differences between these species are not correlated consistently with geographic location, so that they seem to have diverged through assortment of characters. In spite of the various differences in shape, sculpture, size, and color banding between the *Mexipyrus* species, none shows distinctive characters in the male genitalia, where the most useful taxonomic differentia between populations and species would be expected. Hence divergence of the colonies may not be related to reproductive isolation except through their geographic separation.

Other kinds of animals besides the snails show local endemism, although not as spectacularly. About half of the 20 fish species are restricted to the valley, and one cryptic species is specialized to feed on snails. Three forms of turtles are endemic to the basin; this is the highest concentration of endemism among Testudinata known in North America. One of these forms is a semi-aquatic species of *Terrapene*, a genus that is otherwise terrestrial. In these and other groups now under study, the isolation affects aquatic and marsh-dwelling forms most conspicuously.

No direct fossil evidence is available for judging the length of isolation of the endemic snails of the Cuatro Ciénegas area. If degree of taxonomic divergence is proportional to isolation, then the ancestry of some of the fauna reaches deep into the Tertiary, or Mesozoic. *Mexipyrus*, an endemic genus of a widespread subfamily, shares characters of two genera that each have a fossil record; if all three genera diverged from a common ancestor they separated in early Tertiary times. By analogy with other species of Hydrobiidae the local endemic species of *Mexipyrus* have evolved during the last 2 to 3 million years; if so, individual large springs or groups of springs have such antiquity.

Two of the species that do not belong to endemic genera are nonetheless remarkable. *Assimineae* spec. is a rare inland occurrence of a usually coastal, marine family. *Cochliopina milleri*, spec. nov., is related to species of northern Guatemala rather than geographically nearby forms.

The following new groups are known only from the valley of Cuatro Ciénegas:

Cochliopinae: *Cochliopina milleri*, spec. nov.; *Coahuilix hubbsi*, gen. et spec. nov.

Littoridininae: *Duragonella coahuilae*, spec. nov.; *Mexipyrus*, gen. nov., with *M. carranzae*, *M. churinceanus*, *M. escobadae*, *M. lugoi*, *M. mojarrales*, *M. multilineatus*, spp. nov.

Nymphophilinae, subfam. nov.: *Nymphophilus minckleyi*, gen. et spec. nov.

Hydrobiidae?

Mexithaumatinae, subfam. nov.: *Mexithauma quadripaludium*, gen. et spec. nov.

Paludiscalinae, subfam. nov.: *Paludiscala caramba*, gen. et spec. nov.

Appraisal of the fauna has required a substantial review of many groups, including the freshwater Rissoacea of the Western Hemisphere. All of the genera described as Hydrobiidae from North America have been allocated to a subfamily within that group, or have been referred to another family. The family Hydrobiidae, and all North American subfamilies within it, have been diagnosed. All of the South American genera that belong to one of these subfamilies have been so allocated; a few genera without northern relatives are ignored. All of the North American, and some South American forms of the Cochliopinae and Littoridininae have been listed by genera to clarify the geographic distribution of the groups. This taxonomic revision has led to the establishment of the following groups that are new in scope or definition but not always in name. Hydrobiidae

Cochliopinae, subfam. nov., with three new tribes:

Cochliopini, Horatiini, and Clenchiellini

Fontigentinae, subfam. nov.

Lithoglyphinae, subfam. nov.

Littoridininae, subfam. nov.

In numerous attributes of several organ systems the Bithyniidae, generally classified in or near the Hydrobiidae, are radically different. They are transferred to the Viviparacea, and in so doing the value of the radula in indicating affinity among lower Mesogastropoda is sharply questioned.

The brackish-water genus *Clenchiella* ABBOTT, 1948, is classified among Cochliopinae in Hydrobiidae. It is significant in possessing low swellings on the posterior border of the left tentacle, a multispiral operculum with sub-central nucleus, and planispiral shell. This combination of features is found also among marine Vitrinellidae, and provides evidence that the marine family is derived from the Cochliopinae.

Comparison of the fauna from the valley of Cuatro Ciénegas with that of adjacent regions led to two compilations. One is the known fauna of Coahuila, consisting of five species so far as previously published records go. With additions from both inside and outside the Cuatro Ciénegas area this total is increased to 26.

A second compilation is literature on freshwater mollusks from northeastern México (states of Chihuahua, Nuevo Leon, San Luis Potosí, and Tamaulipas) published since the last summary in the "Biologia Centrali-Americana"; and on those from southern and western Texas, and from the Rio Grande drainage in New Mexico, U. S. A. The literature is widely scattered and probably some

has been overlooked, but it is still evident that little is known of this vast region.

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